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ASSESSING FOREST RESPONSES TO CLIMATE CHANGE AND RESOLVING PRODUCTIVITY MEASUREMENTS ACROSS SPATIAL SCALES

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Climate change and productivity measurements in forests

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Informed decisions regarding forest and carbon resources require knowledge of the impacts of environmental changes on forest productivity. We also need to reconcile the diverging productivity estimates that are presently available. This dissertation assembles two publications addressing the impacts of climate change on forest productivity and one exploring the relationship between three estimates of forest productivity.

In the first chapter, I evaluated whether forests have responded to recent changes in climatic conditions. Through combining published evidence I show that forests have responded to changes in the patterns of light, water, and temperatures over the last half of the 20th century. Most published studies showed a positive growth trend. Negative growth trends were found for drier study areas. Conclusions on the greening of the world's forests, are difficult due to poor geographical coverage and measurement method disparity. In the second chapter, I compared three productivity estimation methods (two ground-based and one satellite-based) using 166 sites in Austria. Results of disturbance-free projections show the relevance of each method to actual site productivity and their combined usefulness in identifying the most appropriate scale for monitoring climate forcings. Each estimation method provides information on a portion of the underlying actual NPP. In the last chapter, I explore the effect of three IPCC climate change scenarios on forests of the US Northern Rockies. Results show an increase in growing season length and in water stress, and a decrease in snow quantities and in number of days with ground snow for all forests by 2089. Under the driest and warmest scenario, the majority of the sites became carbon sources, and I identify a water/temperature tipping point, past which system stored carbon drastically declines. For these disturbance-free projections, water availability drove the system.

In this dissertation, I resolve a potential source of conflict among forest productivity estimates; combined, these estimates lead to a broader understanding of productivity. I also present evidence that forests are already responding to climate change, and that more drastic changes are likely in the future.

DEDICATION

I dedicate this dissertation to my friend, partner, and respected colleague, Eliot JB McIntire.

His insights into ecology, his philosophy, and perspective on the world we live in, work in, and study were priceless contributions to this research and to my well-being during the process of completing my PhD. Our many conversations and debates constantly pushed my ideas and research farther, expanding my knowledge and understanding with each occurrence, often under the light of a new perspective. The remarkable patience, love, and understanding he gave during these last five years supported my research and sustained my smile.

Eliot also insured that I did not neglect my love and appreciation for the outdoors during this busy time, and together, we manage to balance work, play, and travel. He followed me to Montana, I now have followed him to Quebec, and I wonder where next?

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PREFACE

Forests contribute significantly to the global carbon budget (Houghton 2007), they influence local and regional meteorological conditions (van der Molen et al. 2006), they affect the global energy balance (Bala et al. 2007), they can change atmospheric circulation (Buermann et al. 2007), and they constitute a substantial part of our national and local economies, not to mention their importance in our quality of life. Yet there is still much to understand about our forest ecosystems. The research presented in this dissertation addresses some salient points that contribute to furthering our understanding and supporting our decision-making processes when it comes to forests. The dissertation itself is composed of three distinct articles, which at the present time are at varying stages of publication in the peer-reviewed literature. Chapter 1 was published in Global Change Biology in 2006 (Boisvenue and Running 2006), Chapter 2 is submitted to Ecological Application, and Chapter 3 is in preparation for submission. Each chapter is organized as a self-contained entity, and this dissertation is therefore organized as such: each chapter addresses a separate question with its own conclusions; tables and figures are organized in three sections relating to each chapter, and so are references.

In Chapter 1 I attempt to establish whether forests have responded to the changing climatic conditions of the last half of the 20th century; in Chapter 2, I explore different measurements of productivity and explain how they related to each other; and in Chapter 3, I analyze baseline projections of forests under three climate-change scenarios varying in their precipitation levels.

Like most research projects, none of these articles is exhaustive. Given the issues explored in this dissertation, the complexity of the systems at play, and our present level of understanding, these issues could not be completely addressed without lifetimes dedicated to their research, as they are constantly changing. The research presented here, however, expanded my knowledge and understanding of forests, of how they are influenced by atmospheric conditions, and of how effectively we presently measure them. It also ingrained in me the importance of broadening our research horizons beyond our

system of interest to expand our understanding of that very system. I hope you will find this dissertation interesting and that it will contribute to broadening your knowledge of forest ecosystems.

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Introduction

Forests and forest production have been an integral part of society throughout human history. In 1662, the Interregnum and English civil war caused a crisis for sources of wood and threatened the restored monarchy. John Evelyn's Silva report (1664), addressing the request of the Royal Society for pertinent information about cultivating trees as quickly as possible, was probably the first book published on silviculture and forest production (http://instruct.uwo.ca/english/234e/site/chrnlgy2.html). The quest for understanding our environment has, over centuries, given us insight into the mechanisms governing forest systems. In the 1640s, the work of both Johannes (Jan) Baptista van Helmont (1577 - 1644), an English clergyman, and physiologist Stephen Hales indicated that plants require air and water to grow (Sinha 2004).

Documented changes in climatic conditions since the middle of the last century (Jones and Mann 2004) coupled with our knowledge of the controls of forest production from forest physiology research lead us to believe that the conditions under which forests have developed in the recent past, conditions that drive production, have changed. However, the impacts of environmental changes on global forest production are uncertain. M.G.R. Cannell's book World Forest Biomass and Primary Production Data (1982), provides a thorough compilation of forest stand level biomass and production data up to 1981.

The main objective of this paper is to review documented evidence in the scientific literature of the impacts of climate change trends since the 1950s on forest productivity. Any references to modelling speculations or experimental manipulations were not considered in this review, only observed and documented impacts on forests were incorporated. Forests respond to both short-term and longer-term variations in the environment (Innes and Peterson 2001) and because of the blurred separation between

natural and anthropogenic atmospheric changes (IPCC, 2001; Innes & Peterson, 2001), we make no distinctions between the two in this paper.

Three types of data form the basis of this review: satellite findings, field-based data from carbon sequestration research, and field-based data from forest management planning and activities. Satellites provide a broad overview of forest production at the regional to global scale (Running et al. 2004), while field observations of the impacts of climate change on forest production give regional and local estimates. Recent monitoring of carbon through net primary production (NPP), net biome production (NBP), net ecosystem production (NEP) and net ecosystem exchange (NEE), promoted by the increasing interest in carbon sequestration, provides a picture of forest productivity status at regional to global scales. An important source of observations of change is above-ground biomass-related measurements such as diameter, height, and tree or stand volume, the common basis for stand-level studies and inventories, which are the basis for forest management planning around the world.

The distinction among NPP, NBP, NEP and NEE is often unclear in the literature. We interpreted our findings following the IPCC (2003) definitions of these carbon measurements. The IPCC (2003) defines NPP as the rate of carbon accumulation in plants after losses from plant respiration and other metabolic processes (necessary to maintain the plant's living systems) are taken into account. It can be calculated as gross primary production (GPP) minus autotrophic respiration. NEP takes into account heterotrophic respiration such as decomposition of dead organic matter, and thus can be measured from the changes in carbon stocks in vegetation and soil or by integrating fluxes of CO_2 in and out of the system (NEE) (Goulden et al. 1996, IPCC 2003). NEP is the accumulation of carbon over a whole ecosystem and over a whole season or other time period (IPCC 2003). NBP refers to the net production of organic matter (e.g., biomass) in a region containing a range of ecosystems (e.g., a biome), including disturbances (IPCC 2003). It can be calculated by summing ecosystems-level NEP over a region and subtracting losses due to disturbances. At the ecosystem scale, carbon losses due to disturbances are relatively infrequent and difficult to quantify. At the biome-scale,

however, disturbances such as fires and forest harvest can be considered processes since they occur on a regular basis in one area or another of the biome (Georgii and Yoshiki 2002). NBP seems to be the most appropriate way to analyze long-term, large-scale changes in carbon (often referred to as a carbon sink or source), while NPP and NEP are more useful measures of carbon at an ecosystem or forest stand-level. Many publications report above-ground NBP (ANBP) without specifying that measurements only considered aboveground carbon. In our review, we have incorporated the distinction between NBP and ANBP.

In this text we first present a concise overview of the climate control of forest primary production. We then provide evidence of how the main controls have changed since the 1950s, followed by the core section of our review, our findings of observed and documented impacts on forest productivity. Finally, we present a brief discussion of the complications inherent in interpreting trends in NPP.

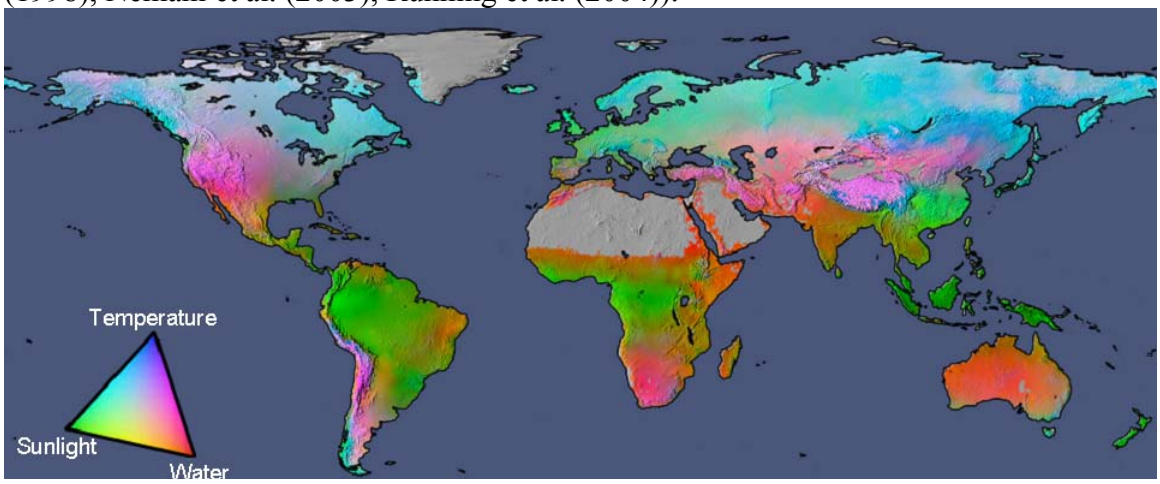
Climate and forest production

Although all biological activity in plants is ultimately dependent on absorbed solar radiation, it is obvious that solar radiation alone does not determine primary productivity. All plants require sunlight, carbon dioxide, and water for photosynthesis. Beyond these basic requirements, the amount of foliage, the light use efficiency of this foliage, water availability, ambient temperature, availability of soil nutrients, and the adaptations of species to extreme temperatures and efficient use of water and nutrients are finer controls of forest productivity (Schulze et al. 2002, Hopkins and Hüner 2004).

The main abiotic controls of primary production (temperature, radiation and water) interact to impose complex and varying limitations on vegetation activity in different parts of the world (Churkina and Running 1998, Nemani et al. 2003, Running et al. 2004). Physiological responses to changes in climate are highly dependent on the limiting factors of a particular site to forest growth. For example, increasing temperature may also increase vapour pressure deficit (VPD) of the air, and thereby increase transpiration rates,

resulting in adverse effects on dryer sites, unless stomata close in response to other changes such as an increase in CO_2, or if increases in night-time temperature exceed increases during the day (Kirschbaum 2004). Figure 1 depicts the distribution of the limiting factors to primary production in terms of water, sunlight and temperature on a global scale. Very few forest types in Figure 1 are solid colours, expressing variability in the dominance of limiting factors within a given year. For example, the productivity of temperate forests of northwestern North America may be radiation- and temperature-limited in winter, temperature-limited in spring and water-limited by midsummer. These controls depend on climate and are expressed as a mosaic of regionally varied impacts on forest systems.

Figure 1.1 Potential limits to vegetation net primary production based on fundamental physiological limits by VPD, water balance, temperature. (From Churkina and Running (1998), Nemani et al. (2003), Running et al. (2004)).



Temperature (heat) controls the rate of plant metabolism which in turn determines the amount of photosynthesis that can take place. Most biological metabolic activity takes place within the range 0 to 50° C (Hopkins and Hüner 2004). There is little activity above or below this range. The optimal temperatures for productivity coincide with 15 to 25° C, the optimal range of photosynthesis (Hopkins and Hüner 2004) and lethal levels are between 44 and 52°C (Schulze et al. 2002). Photosynthesis depends on radiation, increasing with increasing irradiance. Water is a principal requirement for photosynthesis and the main chemical component of most plant cells. In dry regions, there is a linear increase in NPP with increased water availability (Loik et al. 2004). In a study of systems

with nearly steady-state aboveground standing crop, Webb et al. (1983) show an exponential decrease in productivity with decreased water availability. Knapp and Smith (2001) found a strong correlation between ANPP and annual precipitation across North America (22 study sites), but show the interannual variability in ANPP not to be related with precipitation. Contrary to Knapp and Smith (2001), Fang et al. (2001b) show a significant positive relationship between the coefficient of variation (CV) of the Normalized Difference Vegetation Index (NDVI[1]), used as a predictor of NPP, and that of precipitation. The differences in the scope of the data used in the Knapp and Smith (2001) versus Fang et al. (2001b) analyses may be the source of the different findings, however, they may also stem from a difference in the time and space variability of productivity in relation to precipitation, hence, there is a scale issue.

Forest soils and site productivity will likely be affected by changes in both site water balance and temperatures since these affect soil organic matter decomposition rates (Moore et al. 1999, Barrett 2002, Trofymow et al. 2002, Kirschbaum 2004). Increased decomposition rates could result in more readily mineralized nutrients available to plants, which would likely increase photosynthetic carbon gain in nutrient-limited systems (Kirschbaum 2004). An important contribution to forest soils may be the increase in atmospheric N deposition. Atmospheric depositions of N are likely to enhance growth for many temperate coniferous forests sites where N is considered to be the most common limiting nutrient (Breymeyer et al. 1997).

The increase in productivity with an increasing amount of foliage is intuitive. The light use efficiency of foliage, however, is thought to vary across forest types, and even within a single tree canopy, but how it varies across species and time scale is still under debate (Nichol et al. 2002, Guo and Trotter 2004, Lagergren et al. 2005). In a comparison of above ground NPP in deserts and forested ecosystems Webb (1983) found ecosystem type to have some control over abiotic factors in producing above ground NPP but that this influence was not large. Hence, forest ecosystems, like all other ecosystems, are

[1] NDVI = (NIR — VIS)/(NIR + VIS) where NIR is Near InfraRed and VIS is visible light.

mainly at the mercy of abiotic factors (radiation, water, temperature) with some adaptations having small effects, at least for above ground NPP.

There is considerable variability in NPP controls across forests systems throughout the world. Changes in the rainfall patterns are likely to have large corresponding effects on forest productivity in regions where productivity is water-limited (Kirschbaum 2004). Similar statements can be made about radiation and temperature changes. Changes in temperature and precipitation can also change growing season length, an important determinant of NPP in temperate and boreal forests (Kimball et al. 2004). Jolly et al. (2005) developed a phenological-control model using a combination of day length, VPD and minimum temperatures. The model appropriately depicts changes in growing season length regionally and globally, supporting the control that radiation, temperature and water exert on growing season length. White et al. (2005) identify the regions of high latitude North America and Eurasia as indicators of climate change because the productivity in these regions is limited by the combination of climatically controlled factors and affected by compositional atmospheric changes, but is relatively free of other forces that drive of productivity changes such as urbanization, political changes and other land-use changes.

Two patterns of climatic variability that contribute to changes in rainfall and precipitation were prominent in the 20th century: the Pacific Decadal Oscillation (PDO) and the El Niño/Southern Oscillation (ENSO) (Bond and Harrison 2000, Nemani et al. 2003). ENSO- and PDO-influenced climate variables, such as temperature and precipitation, strongly influence interannual variability in NPP (Nemani et al., 2003) and are referred to throughout the following sections. ENSO is the primary driver of temperature variations across the tropics and of precipitation fluctuations for large areas of the Americas and Southeast Asia. PDO and ENSO display similar spatial climate fingerprints but have a very different behavior in time.

Evidence of climatic changes

Global temperature and precipitation trends

Global average temperature increased by 0.6±0.2ºC in the past 100 years, and global average precipitation has increased slightly (Barnett 2001, Houghton et al. 2001, Levitus 2001). The greatest warming, up to 4°C, occurred in winter. Jones and Mann (2004) refer to a recent large-scale warming and their assessment affirms the conclusion that late 20th century warmth is unprecedented at hemispheric and likely, global scales (Jones and Mann 2004). They also point out the regional variability and the dramatic differences between regional and hemispheric/global past trends, which was confirmed by Feng and Hu's (2004) observation that changes in regional and local surface air temperatures and precipitation do not follow these global increases. Some regions, like Austria, exhibited no increase in temperature for latter parts of the 20th century (Hasenauer et al. 1999) while others show dramatic increases in valley bottoms but not at high elevations (Mote et al. 1999, Innes and Peterson 2001, Mote 2003b).

Global radiation trends

Changes to incoming radiation have also been reported. Independent studies reported large increases in incoming solar radiation between 1980s and the 1990s in parts of the world, mainly due to changes in cloudiness (Wielicki et al. 2002, Nemani et al. 2003). Contrary to these satellite analyses, ground-based measurements from thermopile pyranometers suggest that significant reductions in solar radiation reaching the Earth's surface have occurred during the past 50 years, termed 'global dimming' (Stanhill and Cohen 2001). In an analysis of surface observations for the Northern hemisphere Wild et al. (2005) show the dimming not to have persisted in the 1990s but point rather to a widespread brightening since the late 1980s. Pinker et al. (2005) confirm this brightening in their analysis of the amount of solar radiation at the Earth's surface between 1983 and 2001, where they found a decrease until about 1990 followed by an increase in solar radiation. These discrepancies may be attributed to measurement, temporal and spatial scales of the databases analyzed, localized increases or decreases in radiation and perhaps even to increase in diffuse radiation due to Mount Pinatubo's eruption (1991) (Trenberth 2002, Gu et al. 2003, Clark 2004, Lewis et al. 2004a).

Global trends in CO_2

Although CO_2 is not the only atmospheric gas that has increased since the 1950s, its multi-faceted role in primary production, the potential for plant carbon sequestration, and the potential effect it has on global temperatures, makes CO_2 the focus of much research. Direct measurement of CO_2 at Mauna Loa Hawaii clearly show a 55 μmol mol^{-1} increase from 1959 to 2001 an increase of more than 16% during that time period (Keeling and Whorf 2002). Of the approximately 760 Gt C in the atmosphere, photosynthesis by terrestrial vegetation removes approximately 120 Gt, almost 16% of the atmospheric content annually, but can return an equivalent amount through autotrophic and heterotrophic respiration (Prentice et al. 2001, Schimel et al. 2001).

Trends by forest types

Analysis of station temperature trends during 1961-1990 indicate pronounced warming over substantial areas of the boreal forest in Alaska, northwestern Canada and northern Eurasia (Chapman and Walsh 1993). Air temperatures that regulate growing season dynamics have increased over temperature-limited regions of northwestern Europe (Myneni et al. 1997) and an increase in temperatures and in growing degree days, defined for our purposes here as daily temperatures above 0 ◦C, of +1.7°C and 16 % respectively, were documented for the northeast of British Columbia (BC), Canada (Mote 2003a).

In the temperate forests of the Pacific Northwest of North America, changes in temperature (+0.8°C) and precipitation (+14%) exceeded the global average during the 20th century. Even within that region finer scale regional variations depict the patterns of temperature in the Pacific Northwest more accurately: during the 20th century, average temperatures warmed by 0.6°C on the coast of BC and 1.1°C in the interior of the province (Mote 2003a), and precipitation has been increasing by 2 to 4% per decade, primarily in the winter. A 50% increase in precipitation has been recorded in northeastern Washington and southwestern Montana during the 20th century (Mote 2003a). A large part of the recent increase in temperatures reflects a rise in minimum temperatures whereas maximum temperatures may remain stable or actually decrease, especially during the summer season. Hence, systems limited by maximum temperature (as the

Canadian Cordillera may be) may not have shown any corresponding changes in productivity (Luckman et al. 2004).

Over most of the western US, winter snow fall dominates the precipitation patterns (Mote et al. 2005). Climate and snow data for the U.S and Canada showed a decline in mountain spring snow packs by approximately 30% since 1950 indicating earlier and/or winter melt (Mote 2003). Analyses show climatic trends to be the dominant factor in snow pack decline, as opposed to changes in land use, forest canopy, or other factors (Mote 2003a, Hamlet et al. 2005). Snow accumulation, along with soil storage and groundwater, are the primary mechanism by which water is stored and transferred to the relatively dry summer of western North America (Hamlet et al. 2005) and hence, snow pack is a critical determinant to limitations imposed on tree growth and other ecological processes. The reported declines in snow pack are further corroborated by observed changes in stream flow toward earlier peak snowmelt, lower summer flow, and higher winter flow (Mote 2003, Mote et al. 2003, Mote 2003a, Hamlet et al. 2005, Mote et al. 2005). Taken together, these results emphasize that hydrologic resources are already responding to changes in climate in North America's west.

As in boreal forests, changes in temperature are reflected in a changing number of growing degree days in temperate forests. Growing degree days in BC increased by 13% on the coast and in the southern interior, and by 5% in the central interior of the province (Mote 2003a). In a study of 88 years of data, White et al. (1999) showed that for individual sites in the eastern deciduous broadleaf forests of the USA, the length of the growing season regularly varied by more than fifteen days. Hence, what constitutes a change over time within the normal variability of growing season length requires careful consideration of the site or area's historic variability to depict a trend. Nevertheless, Cayan et al.'s (2001) findings seem to confirm an advance in the timing of spring since about 1950 in much of North America, while Feng and Hu's (2004) results show an increase in growing season length across the western USA and a decreasing trend from the U.S. Great Plains to the East Coast. A study by Inouye et al. (2000) showed no significant change in the calendar date of the beginning of the growing season at high

altitude in the Colorado Rocky Mountains over the last quarter of the 20th century. Data from temperate eastern China show the growing season to have been extended by 1.4-3.6 days per year in the northern reaches and by 1.4 days per year across the whole area between 1982-1993 (Chen et al. 2005). According to Peterson and Peterson (2001) and Peterson et al. (2002), the lighter snow packs of PDO periods in the Pacific Northwest brought an earlier start to the high-elevation growing season. However, at lower elevations where summer moisture stress limits productivity, growth was negatively correlated with PDO (Peterson and Peterson 2001, Peterson et al. 2002). In their analysis of temperate eastern China, Chen et al. (2005) found growing season length to correlate significantly with spatial patterns of mean air temperatures in the spring and autumn. The effects of an increased growing season length, much like precipitation and temperature, are dictated by regional conditions and site specific limiting factors to productivity.

Tropical forest regions show temperature increases averaging 0.26 ± 0.05°C since the mid-1970s (Clark 2004, Malhi and Wright 2004) and a strong variation in long-term rain trends (Houghton et al. 2001, Malhi and Wright 2004). Overall precipitation appears to have declined in tropical rainforest regions at a rate of $1.0 \pm 0.8\%$ ($p<0.05$) per decade since 1960 (Malhi and Wright 2004). This pan-tropical decreasing trend in land surface measurements of rainfall, however, is primarily driven by a strong and significant decline in rainfall in the northern African tropics (3-4% per decade) (Houghton et al. 2001, Malhi and Wright 2004). Rainfall only declined marginally in tropical Asia and showed no significant trend in Amazonia (Malhi and Wright 2004).

Productivity response

Given our knowledge of the mechanisms driving forest productivity and the changes outlined in the previous section, we expect to see a detectable forest response to changes in climatic factors. Much like changes in temperature, precipitation and radiation, productivity responses of forests have been measured at different time and spatial scales using a variety of measurement tools. In this section, we first outline reported changes in productivity at a large spatial scale, which mostly comprises satellite and global

estimates, then present regional and/or country-level estimates found in the literature followed by trends from ground-based estimates. Table 1 summarizes the findings in this section.

Global and continental trends

According to Nemani et al. (2003), globally, NPP seems to have increased by 6% (3.4 PgC) over the period from 1982 to1999 but with declines during all three major ENSO events. Other studies analyzing satellite-driven measures of vegetation greenness (NDVI), a surrogate for photosynthetic activity (Field et al. 1995, Prince and Goward 1995, Slayback et al. 2003), also indicated reduced productivity in tropical ecosystems in warmer years (Braswell et al. 1997, Asner et al. 2000, Los et al. 2001), which are associated with ENSO. NDVI is a remotely observed variable that responds strongly to healthy, green vegetation and is approximately linearly related to the fraction of photosynthetically active radiation absorbed by green vegetation (Sellers 1987). It is, therefore, a good proxy for photosynthetic activity (Slayback et al. 2003) and was shown to be highly correlated with NPP (Field et al. 1995, Prince and Goward 1995). NDVI measurements used for vegetation monitoring, seem to also support an increasing trend in photosynthetic activity during 1982-1999 (from 0.0015 to 0.0045 NDVI units/year), with trends generally higher in the 1990s than in the 1980s at global latitude bands from 35 to 75° north (Slayback et al. 2003). According to Slayback et al. (2003), trends in North America and Eurasia for the 1980s were roughly comparable, while in the 1990s the North American trends were generally higher. Large areas of Canada, Europe, and northern Asia seemed to be experiencing a significant positive trend across all vegetated land covers (Slayback et al. 2003), not just forest systems. The carbon balance of boreal deciduous and conifer forests has been shown to be sensitive to seasonal and interannual climatic variability (Arain et al. 2002). White et al. (1999) confirm that a long growing season does increase NEP, GPP and evapotranspiration (White et al. 1999). Longer growing seasons reported increased carbon storage in aspen boreal forests (Chen et al. 1999) and in northwestern Europe (Lucht et al. 2002) where increased air temperatures have promoted earlier plant growth (Myneni et al. 1997). Nemani et al. (2003) attributed the largest increase in NPP in the last two decades of the 20th century to tropical

ecosystems. In this analysis, the Amazon rain forest accounted for 42% of the 6% global increase in NPP. Some studies attribute this increase to increases in solar radiation, owing to declining cloud cover in these predominantly radiation-limited forests (Trigo et al. 2002, Wielicki et al. 2002, Graham et al. 2003, Nemani et al. 2003), while others attributed it to more local changes in cloud cover as well as increases in CO_2 level and air temperatures (Lewis et al. 2004b). Graham et al. (2003) attributed the response in productivity level to the more tightly coupled NPP and soil respiration processes in tropical climates compared with ecosystems in other latitudes.

Regional trends

The analysis of satellite data accompanied by process modelling showed an increase in China's NPP between 1982-1999 (Fang et al. 2003). However, forests were only one contributor to this estimate and, although they are considered to be a large contributor to this increase in NPP (Fang and Wang 2001), the spatial variability of NPP over the vast extents of China is very high (Yue et al. 2005) with increases up to 31% in NPP in certain areas and losses in NPP in areas of rapid urbanization (Fang et al. 2003). In an analysis based on forest inventory data, Fang et al. (2001a) showed Chinese forests to have been a carbon source between 1949-1980 (0.022 PgC/year) and planted forest a sink between late 1970s and 1998 (up to 4.75 PgC/year in 1998) (Fang et al. 2001a).

Regional studies in North America and in the USA reported increases in NPP of 2 to 8% between 1982-1998 (Hicke et al. 2002). Changes in North America are thought to stem from increased growth by natural vegetation with increased precipitation and humidity, especially during the 1950-1993 period (Nemani et al. 2002) and from the increase in air temperatures stated earlier that regulate the growth-season dynamics over temperature limited regions (Myneni et al. 1997, Lucht et al. 2002). Reporting on the terrestrial carbon sink for the contiguous United States, Pacala et al. (2001) estimated a gain of 0.3-0.6 PgC/a during the 1980s. Although this estimate is not exclusive to forests, forests are thought to be a major contributor (Pacala et al. 2001, Janssens et al. 2004).

Table 1.1. Summary of published change in forest productivity under recent climate change. Variables are: Net Primary Production (NPP), Net Ecosystem Exchange (NEE), Net Biome Production (NBP), aboveground NPP (ANPP), aboveground NEP (ANEP) and aboveground NBP (ANBP).

Variable	Change	Time scale	Spatial scale	Data type	Reference
ANPP	+	1982-1999	globe	satellite	Nemani *et al*. 2003
ANPP	-	ENSO years	tropics	satellite	Nemani *et al*. 2003
ANPP	-	ENSO years	tropics	satellite	Braswell *et al*. 1997
ANPP	-	ENSO years	tropics	satellite	Asner *et al*. 2000
ANPP	-	ENSO years	tropics	satellite	Los *et al*. 2001
NDVI	+	1982-1999	northern hemisphere	satellite	Slayback *et al*. 2003
ANBP	+	growing-season	boreal aspen	land-flux tower	Chen *et al*. 1999
ANPP	+	growing-season	north-western Europe	satellite	Lucht *et al*. 2002
ANPP	+	1982-1999	China	satellite	Fang *et al*. 2003
ANBP	-	1949-1980	China	land-biomass	Fang *et al*. 2001a
ANBP	+	1970s-1998	Chinese planted forests	land-biomass	Fang *et al*. 2001a
ANBP	+	1982-1998	North America	satellite	Hicke *et al*. 2002
ANBP	+	1945-1990	USA	combined types	Houghton *et al*. 1999
NBP	+	1980-1989 1990-1994	USA	atmospheric and land-flux tower	Pacala *et al*. 2001
NBP	+	1990s	European forests and grasslands	combined types	Janssens *et al*. 2004
ANPP	+	recent	Canadian and Alaska boreal forests	combined types	Innes and Peterson 2001
ANPP/ANBP	-	1951-2000	Canadian prairies boreal aspen	land-biomass	Hogg *et al*. 2005
ANPP	+	since 1970	boreal/tundra forest	land-biomass	Gamache and Payette 2004
NBP	+	1950-1999	European forests	land-biomass	Nabuurs *et al*. 2003
ANPP	+	20th century	Canadian Cordillera	land-biomass	Luckman *et al*. 2004
ANBP	+	during PDO events	Pacific Northwest	land-biomass	Peterson and Peterson 2001
ANBP	+	during PDO events	Pacific Northwest	land-biomass	Peterson *et al*. 2002
ANPP	-	1926-2001	Northwest Russia	land-soil fluxes	Lawrence *et al*. 2005
ANPP/ANBP	+	20th century	Scots Pine in Lapland	land-biomass	Mielikäinen and Sennov 1996
ANPP/ANBP	**0**	20th century	Scots Pine southern Finland	land-biomass	Mielikäinen and Sennov 1996
ANPP/ANBP	+	20th century	Sweden	land-biomass	Elfving *et al*. 1996
ANPP/ANBP	+	1953-1992	Swedish forest	land-biomass	Eriksson and Karlsson 1996
ANPP/ANBP	+	since 1960s	Scott Pine and Norway spruce in Sweden	land-biomass	Eriksson and Karlsson 1996
ANPP/ANBP	+	1920s-1990	Danish beech forest	land-biomass	Skovsgaard and Henriksen 1996
ANPP/ANBP	+	1975-2000	eastern Germany spruce and beech	land-biomass	Uhtheim1996 Wenk and Vogel 1996
ANPP	+	last 150 years	France	land-biomass	Badeau *et al*. 1996
ANPP/ANBP	+	since 1905	Toppwald Switzerland	land-biomass	Bräker 1996
ANPP/ANBP	+	20th century	Norway spruce in the Swiss Jura	land-biomass	Schneider and Hartman 1996

ANBP/NBP	+	1947-1995	Japan	land-biomass	Fang *et al*. 2005
ANPP/ANBP	+	± 100 years	various parts of Switzerland	land-biomass	Zingg 1996
ANPP/ANBP	+	since 1961	Austria	land-biomass	Schadauer 1996
ANPP/ANBP	+	since 1961	Austria	land-biomass	Hasenauer *et al*. 1999
ANPP/ANBP	+	1947-1990	Slovanian beech forests	land-biomass	Kotar 1996
ANPP/ANBP	+	last 150 years	Spanish forests	land-biomass	Montero *et al*. 1996
NEP/NBP	+	110 years	European beech	land-biomass	Bascietto et al. 2004
ANPP/ANBP	+	1970-1990	Portugal maritime pine	land-biomass	Tomé *et al* 1996
ANPP/ANBP	-	1970-1990	Portugal eucalyptus	land-biomass	Tomé *et al* 1996
NEP/NBP	+	1982-2001	Thuringian managed coniferous forests – high elevation temperate conifer forests of Central Europe	land-biomass	Vetter *et al*. 2005
ANBP	+	1970s and 1980s	Austria, Finland, Sweden, Germany, France and Switzerland	land-biomass	Kauppi *et al*. 1996
ANBP	+	1970s and 1980s	Austria, Finland, Sweden, Germany, France and Switzerland	land-biomass	Spiecker *et al*. 1996
ANPP/ANBP	+	1975-1996	old growth tropical forests	land-biomass	Phillips *et al*. 1998
NPP/NBP	+	1980-1989	tropical forests	land-flux tower	Malhi and Grace 2000
NBP	+	1990s	northern extratropical areas	land-flux tower	Schimel *et al*. 2001
NBP	**0**	1980s	northern extratropical areas	land-flux tower	Schimel *et al*. 2001
NBP	**0**	1980s & 1990s	Tropical land areas	land-flux tower	Schimel *et al*. 2001
ANBP	+	1971-2002	tropical forests across South America	land-biomass	Baker *et al*. 2004
NEP	-	1984-2000	Parà, Brazil	land-biomass	Miller *et al*. 2004
ANPP/ANBP	+	1971-2002	tropical forest across South America	land-biomass	Lewis *et al*. 2004b

Trends from ground-based estimates

Boreal forests Changes in vegetation over centuries to millennia in Alaska suggest that the magnitude of ecological response to global climate change is greater at high latitudes than at low latitudes (Ager 1997). For example, paleoaeobotanical evidence indicates that 6,000 years ago boreal forests extended north of the modern tree line, apparently in response to high-latitude warming resulting from variations in the Earth's orbit (Foley et al. 1994). The expanded boreal forest, which replaced the tundra, is thought also to have affected climate by significantly reducing surface albedo (Foley et al. 1994). This apparent plasticity in boreal forests to changes in climate seems to be detectible in forest productivity measurements given the recent changes in climate. A number of phenomena have already been observed that suggest that Canadian and southern Alaskan forests are

responding to recent warming. These include increases in boreal forest productivity, accelerated seasonal development of some insects, changes in the distribution of insect pests, and provenances from slightly warmer areas out-competing local provenances (Innes and Peterson 2001). In northeastern BC, Canada, mature lodgepole pine trees are succumbing to *Dothistroma* needle blight, which is unprecedented (Woods et al. 2005). Woods et al. (2005) identified a clear mechanistic relationship between observed climate trends and host-pathogen interaction. Although most documented evidence points to increases in productivity, decreases have also been reported. A tree-ring analysis of boreal aspen over a large tract (1800 km X 500 km) along the northern edge of the Canadian prairies, showed that during 1951-2000 the region's aspen forests underwent several cycles of reduced growth, when mean stand basal area increment decreased by about 50% (Hogg et al. 2005). This was partially due to increased insect activity but was also attributed to climate changes.

Nugesser et al. (1999) suggests that current methods for forest productivity measurement may be underestimating productivity in boreal forests and Wirth et al. (2002) maintain that changes in site productivity in fire-dominated systems like the boreal forest remain indiscernible due to the large variability in above-ground NPP caused by disturbances. In the northern forest-tundra sites of the province of Québec, Canada, a recent increase in height growth and a positive trend in leader shoot elongation were reported (Gamache and Payette 2004). These increases were not observed in the southern forest-tundra and suppressed height growth of spruce seemed to be more prominent in the southern parts of this systems. A European study by Sinkevich and Lindholm (1996) showed similar observations for the northern reaches of trees in taiga forests in the 1990s with the increment variability in the mid-taiga zone presenting increments characteristic of the northern reaches of the taiga. The interpretation of the reported growth patterns in the southern taiga may be misleading as these forests have shown cyclical patterns of 30-year growth-increment decreases between the mid-taiga and north-taiga stands (Sinkevich and Lindholm 1996).

The general increasing trend in observed NPP is positive for boreal forests and supports the more general and global satellite-based analyses.

Temperate forests Temperate forests have a long history of structured management and forest inventories, more so in European than North American forests. For the period between 1950 and 1999, Nabuurs et al. (2003) report an almost constant increase from 0.03 Pg C/year in the 1950s to 0.14 Pg C/year in the 1990s in NBP of European forests. The Canadian Cordillera did show an increase in growth but not in the two last decades as reported in satellite-based studies (Luckman et al. 2004). Temperature sensitive chronologies showed maximum growth in the mid 20th century rather than in the last few decades (Luckman et al. 2004). These conclusions, however, are based on dendrochronological studies and are thought to reflect regional rather than local climate signals. Again, this illustrates the importance of scale in determining general trends. During a PDO event, which brings warm winters and light snow packs to the Pacific Northwest, USA, growth was positively correlated with PDO in sites where trees are not typically constrained by summer moisture stress e.g., near upper tree line in Oregon and Washington (Peterson and Peterson 2001, Peterson et al. 2002).

Lawrence et al. (2005) found a decrease in diameter growth and a suppression of climate-tree growth relationships in Norway spruce but this decrease coincided with a flux in local industrial pollution. Most studies in northern Europe showed an increase in productivity. In Lapland, Scots pine showed increases in diameter for most forests in the 20th century with increments ranging from 0.85 to 1.5 mm, as compared to the 19th century where increments ranged from 0.45 to about 1.4 mm, with more than half the observations below 1.0 mm (Mielikäinen and Sennov 1996). Scots pine in southern Finland, where the nitrogen deposition is many times higher than in the north, showed no detectable trends in the radial increment while aging stands at sites near Saint-Petersburg, where N deposition has increased to 25 kg/ha/year, did not show the normally observed decrease in current annual volume increment of mature stands during the last few decades (Mielikäinen and Sennov 1996).

The Swedish National Forest Inventory showed a highly significant annual increase in both height and basal area growth (0.5-0.8%) for the period 1953-1992 (Elfving et al. 1996) and site indices (SI), a measure of site quality, have increased for both Scots pine and Norway spruce during the last decades by 0.05-0.11 m/year for spruce and with a difference of 2.5 m with expected SI in pine by the 1980s (Ericksson and Karlsson 1996). SI of beech forests in Denmark also showed an increase between 1920s-1990 of 3.6 m (at reference year of 100) (Skovsgaard and Henriksen 1996) and a general increasing trend in height growth within age classes was observed on both spruce and beech over the last quarter of the 20th century in eastern Germany (Untheim 1996, Wenk and Vogel 1996). SI, despite its shortcomings (Nicholas and Zedaker 1992), is a much-used measure of productivity in forest management (Vanclay 1992). SI has been considered to be constant for species on a given site (Clutter et al. 1983) and changes in this estimate undermine the premise that supports classical growth and yield projections.

In their analyses of Swedish long-term yield experiments, Ericksson and Karlsson (1996) conclude that site productivity has increased in most parts of Sweden during the last 30-40 years. The basal area and height increases do not appear to have influenced the established height growth development patterns that continued to develop according to site curves on permanent sample plots both in Sweden and in Norway (Elfving et al. 1996). Much like the previous mentioned Finnish and Russian studies, these increases are partly attributed to the increase in N atmospheric deposition (Elfving et al. 1996, Ericksson and Karlsson 1996). A comparison of average temperatures and precipitation levels across Sweden from the earlier and latter part of the century show no significant differences between the two time periods in either precipitation or temperatures (Eriksson 1982, 1983). This lack of climatic trend either suggests that averages of daily temperatures and precipitation levels may not be good indicators of changes in site productivity and that the range and extreme events of both abiotic factors may play a more important role in the changes in productivity, or that other factors, such as growing season length combined with N deposition, may be partially responsible for the changes.

Dendrochronological studies in France showed an increasing growth trend in the past 150 years of +50% to +160% depending on species and location (Badeau et al. 1996) with no specification of the portion of this change that occurred in the latter half of the 20th century. This surprising increase was scrutinized by the authors for biases and pre-corrected for the effect of aging. No overarching biases seem to undermine the reliability of data but some localized as well as potential biases were identified (Badeau et al. 1996). It seems appropriate, given the authors' efforts to identify biases, to at least assume that the growth trend is positive and large. After removing the variation in growth caused by short-term climate fluctuations, a case study in Toppwald, Switzerland, also showed an improved growth trend since the beginning of the 20th century (from 4 to 49% of the growth variance) and increased growth in the 1980s (Bräker 1996). An increase of the diameter and basal area increment can be shown for various tree species and for various forest structures in different areas of Switzerland (Schneider and Hartmann 1996, Zingg 1996). In Austria, studies show current annual increment of basal area to have increased since 1961 with a maximum increase in the 1970s and 1980s of 17%, as well as a significant increase in diameter increment obtained from 1179 cores of Norway spruce across Austria with a long-term trend increasing in diameter growth over the 20th century (Schadauer 1996, Hasenauer et al. 1999). The 1970s and 1980s increases were partially attributed to an increase during that time in the length of the temperature-controlled growing season (Hasenauer et al. 1999). Variation in growth responses to increased precipitation between aspects, with some aspects showing higher sensitivity than others, has also been reported in tree line and timber line studies in Austria (Oberhuber 2004), emphasizing that various site-specific controls are at play in these overall positive responses.

Beech forest in Slovenia have shown growth trends surpassing those of yield tables with current annual increment increases of 3.1 m^3/ha in 1947 to 5.3 m^3/ha in 1990 (Kotar 1996). Spanish forest growth trends have also been increasing for the last 150 years but Montero et al. (1996) only partly attributed the change to increased site productivity. Analyses of carbon sequestration trends showed higher than expected levels of carbon sequestration in 110-year old beech forests in Europe (Bascietto et al. 2004). Forests in

northern Spain were accumulating carbon at an average rate of 1.46 Mg C/ha/year from 1972/1973 to 1986/1988 (Rodríguez Murillo 1997) but changes in forest management and land use throughout the region make it hard to discern if forest have actually increased in productivity. Rodríguez Murillo (1997) concludes that increases in the growing stock could be considered compatible with "normal" stand evolution.

Exploratory analysis of growth trends in Portugal did not reveal positive growth trends for volumes of Maritime pine and eucalyptus poplar between 1970 and 1990 (Tomé et al. 1996). Maritime pine did show positive trends in dominant height (≈ + 4.5 m in dominant height) but the trends were negative for eucalyptus (≈ - 12 m in dominant height). The negative trend seems to be related to decreasing amounts of precipitation on these dry sites during the growing season (spring and early summer) during those decades (Tomé et al. 1996).

For Europe as a whole, forest growth trends are positive, although a few cases showed no trends, and some sites with extreme growth limitations such as increased temperatures on water-limited sites, showed a decrease in productivity (Lucht et al. 2002). Based on a point-in-time estimate, the terrestrial carbon sink of Europe during the 1990s is believed to have amounted to 0.1-0.2 Pg C/year (Janssens et al. 2003), and forests are considered a major contributor to this sink (Janssens et al. 2004). Vetter et al. (2005) attributed the increase in productivity (measured in NEP) of high elevation temperate conifer forests of Central Europe to the increase in N deposition between 1982-2001 and the increase in conifer forests at mid- and low-elevations to CO_2 fertilization for (Vetter et al. 2005).

Synthesis compilations of growth and yield data to identify changes in productivity in the light of recent climate change, such as the ones available for Europe, are scarce for other temperate regions of the world. Holman (2004) deciphered widespread positive growth correlations at large spatial scales in the forests of the Olympic Mountains of Washington, USA, suggesting that they are responding to an overarching climate-growth signal, despite the blurring effect of many growth-limiting factors acting at the local scale (Holman and Peterson 2006). A biomass accumulation analysis of Japan's forest from

1947 to 1995 showed an increase in both aboveground and total biomass (26.7 to 43.2 MgC/ha and 33.9 to 56.6 MgC/ha respectively) (Fang et al. 2005). In a smaller scale study of a deciduous forest in New England , USA, Goulden et al. (1996) attributed the variation to changes in photosynthesis and respiration with shifts in photosynthesis associated with the timing of leaf expansion and senescence, and respiration shifts with anomalies in soil temperature, deep snow in winter, and summer-drought. The same mechanisms may be acting at the continental scale expressing themselves in overall trends within the local variation.

Data support forest productivity increases across temperate North America, Northern Europe, most of Central Europe, some parts of Southern Europe and Japan (Kauppi et al. 1992, Spiecker et al. 1996, Myneni et al. 1997, Fang et al. 2005), and generally corroborate the initially stated increases in NPP detected from satellite-based analyses, although local conditions cause exceptions.

Tropical forests Until recently, the prevailing view has been that old-growth tropical forests are likely to have been acting as a substantial carbon sink over the recent decades, increasing their NPP (Phillips et al. 1998, Malhi and Grace 2000, Prentice et al. 2001, Schimel et al. 2001, Baker et al. 2004). Presently, there is much debate about the productivity of tropical forests, and existing data are insufficient to support any firm conclusion. Change in above-ground biomass is just one component of net forest carbon balance, it is the most commonly measured one due to ease of measurement, and to date, no tropical rain forest seems to have a complete assessment of total carbon stocks and their change though time (Clark 2004, Houghton 2005).

Data from a few eddy covariance (tower-based) studies of whole-forest CO_2 exchange have been interpreted as evidence that old-growth tropical rainforests are currently acting as moderate to very strong net carbon sinks (e.g., Malhi and Grace, 2000). Years of anomalously poor tree growth at La Selva rain forest site in Costa Rica were years of peak inferred net emissions from the terrestrial tropics, and both field based and remotely sensed growth records were significantly related to annual temperatures and ENSO

(Clark 2004). Stand and tree-level response to annual climate variations have been recorded at La Selva (Clark and Clark 1994, Clark et al. 2003) with the greatest tree growth occurring during the two coolest years and the lowest growth rates during the record-hot ENSO year 1997/98 with differences of 61-278% between years of greatest and lowest growth rates. Growth rates were intermediate in years of intermediate temperatures (Clark et al. 2003). Baker et al. (2004) indicated a net increase of 0.59±0.31MgC/ha/year in above-ground biomass in forest plots in western Amazonia and even greater net increases in forest plots on river floodplains (1.16±0.39MgC/ha/year). Comparatively, in central and eastern parts of the Amazon, a small but significant net biomass increase was found (0.37±0.34 MgC/ha/year) (Baker et al. 2004). Biometrical measurements from an old-growth forest in Parà, Brazil, showed the forest to be either a source or a moderate sink between 1984 and 2000 (Miller et al. 2004).

An analysis of 50 long-term monitoring plots across South America spanning from 1971-2002 showed increases in tree and stand basal area (BA) (0.1±0.04 m^2/ha/year) during this time period (Lewis et al. 2004b). In relative terms, the pools of BA and stem density increased by 0.38±0.15% and 0.18±0.12%/year respectively, and stem density (number of stems per ha) increased significantly over time (+0.94±0.63 stems/ha/year) (Lewis et al. 2004b). The fluxes in and out of these pools increased by an order of magnitude more, and gains consistently exceeded mortality-losses. The authors conclude that this implied a continent-wide increase in resource availability, which is increasing NPP and altering forest dynamics (Lewis et al. 2004b). Field observations of mortality rates during 1982-85 and 1985-90 in Barro Colorado Island in Panama, showed unexpected results: canopy trees showed the highest mortality of three group types studied during a dry 1982-1985 period while small trees and shrubs showed no difference between the periods (Condit et al. 1995). During drought years, forest-wide mortality rates were 2% more in the larger size class. Tropical forest plot data from both the neotropics and the palaeotropics show large increases in forest-wide tree mortality associated with the very strong ENSO events of 1982/83 and 1997/98 (Clark 2004) and localized species-specific effects (Williamson et al. 2001). Elevated mortality rates, which increased with tree size, were also seen in trees of unburned rainforest in East

Kilimantan during the 1982/83 ENSO with 37% of trees >60 cm in diameter found dead on ridge tops and 71% on slope plots (Leighton and Wirawan 1986). According to Clark (2004), tropical forests have already experienced notable shifts in floristic composition and in tree size structure owing to these selective mortality patterns of single strong ENSO. Clark (2004) interpreted the general finding of a sharp increase in tree mortality in the strong ENSO events of recent decades to mean that tropical old-growth forests around the world are already being strongly negatively affected by current levels of temperature and drought stress.

Discussion

According to both field and satellite-based data found in the literature, the climatic changes in the last 55 years seem to have a generally positive impact on forest productivity on sites where water is not strongly limiting. The many interacting factors preclude the identification of one factor causing these changes as each site has specific, and possibly unique, combinations of factors, however, the changes in productivity correspond to reported changes in temperature, precipitation, and radiation. Our incomplete understanding of the mechanisms and processes in the forest system itself (Ryan 1991, Ryan et al. 1996, Thornley and Cannell 2000, Landsberg 2003, Mäkelä 2003, Magnani et al. 2004) is an important obstacle to the interpretation of these measured impacts. In this section, we outline some other considerations in the interpretation of these findings.

Forests within a changing atmosphere

CO_2 The atmospheric system has not only experienced changes in temperature, precipitation, and radiation, but in CO_2 concentration and pollutants between 1950 and 2005 (Keeling et al. 1976, Keeling et al. 1995, Innes and Peterson 2001). Current global CO_2 is approximately 380 ppm, an increase of about 65 μmol mol^{-1} since the 1950s (Keeling and Whorf 2002). How forests will respond to rising levels of CO_2 in the long term is still uncertain but the present overall response is positive. A median increase of 23% in net primary production has been recorded across sites exposed to elevated CO_2

(550 ppm) in comparison to control sites (370 ppm) since the inception of the Free Air CO_2 Enrichment site (FACE) experiments (Norby, in press). Assuming a linear interpolation of these FACE site results, the 65 μmol mol^{-1} increase since the 1950s would imply approximately a 4% increase in net primary production.

Nowak et al. (2004) tested several early hypotheses on the response of ecosystems to elevated CO_2. Among these were the hypotheses that acclimatization of photosynthesis would occur most prevalently where N is limiting, that productivity response would be greater in drier ecosystems and in drier years for more humid ecosystems, that NPP at FACE sites should vary around a mean increase of 20% (at 550 ppm) and that non-woody functional groups should be more responsive than woody plants. As expected the leaf CO_2 assimilation and the ecosystem primary production increased across all species. The primary production observations, however, are mixed and are overall less than the hypothesized 20%. Downregulation of photosynthesis happened in a number of FACE experiments but not in all species and not consistently in species among sites. The hypothesis about differing responses depending on site water levels was not well supported but the predicted increase in productivity enhancement with N availability was well supported. Nowak et al. (2004) found no consistent support for either the resource-based or the plant functional type response model to CO_2.

Wittig et al. (2005) evaluated GPP of fast-growing *Populus* species (three years from establishment to canopy closure) in response to elevated CO_2 and found that GPP increased dramatically in the first year but markedly less so in the subsequent years. Hättenschwiler and Körner (2003) similarly found accelerated growth in trees over a 30-year period of elevated CO_2 exposure, with most of the accelerated growth happening at young stages of development. The findings of Wittig et al. (2005) and Hättenschwiler and Körner (2003) suggest differing responses of trees at different developmental stages and add another obstacle to a blanket statement about the response of forest productivity to elevated CO_2. Hättenschwiler and Körner (2003) also suggest that trees exposed to higher CO_2 levels seems to be more tolerant to drought stress. Körner (2000) concluded that besides a stimulation of photosynthesis, the most robust finding on plant responses to

elevated CO_2 are changes in active tissue quality (wider C/N ratio) and effects on community dynamics. In their 2005 analysis based on FACE data, Körner et al. (2005) found an immediate and sustained enhancement of carbon flux in mature temperate forest trees but, contrary to expectations, found no overall stimulation of growth or litter production after four years, hence, forests seem to be "pumping" carbon through faster with no net gain in biomass (NEP).

More factors may be at play in CO_2 productivity responses. Kozovits et al. (2005) found that the type of competition (intra versus interspecific) changed the response of trees to elevated CO_2. Through scenario modelling of CO_2, O_3, temperature and precipitation, Hanson et al. (2005) found a change in response direction of annual NEE between single factor and combined factors modelling and also found differing response when adjustments were made for observed physiological responses to these changes. DeLucia et al. (2005) found an increase in NPP and NEP in both loblolly pine and deciduous sweetgum forests, but also found an increase in plant respiration that reduced the NPP (not unlike Körner et al.'s (2005) finding of carbon "pumping") and more so in the pine than in the deciduous forest. DeLucia et al. (2005) warn that greater allocation to more labile tissues may cause more rapid cycling of C back to the atmosphere.

The need to elucidate changes in stand-level biogeochemical cycling requires a focus on large-scale long-term experiments such as FACE sites. As the literature shows, there is no clear answer as to whether rising CO_2 concentrations will cause forests to grow faster and store more carbon (Körner et al. 2005). The response to increasing atmospheric CO_2 confounds our historical understanding of the effects of changes in temperature, precipitation, and radiation, on forest productivity response.

O_3 and pollutants The photochemical oxidant O_3 and pollutants such as SO_2 have been shown to damage plants (Kita et al. 2000, Potter et al. 2002, Ashmore 2005), but the combined effects of pollutants, CO_2 levels, temperatures and changes in precipitation are not mechanistically well understood (DeLucia et al. 1994, DeLucia et al. 2000, Kirschbaum 2004, Ashmore 2005). Global annual background concentration of ground-

level O_3 is about 20-25 ppb (McCarthy et al. 2001). Background concentrations in Europe during the 20th century have increased from 10-15 to 30 ppb (McCarthy et al. 2001). In the northern hemisphere as a whole, trends in concentration of O_3 since the 1970 show large regional differences: increases in Europe and Japan, decreases in Canada and only small changes in the U.S. (McCarthy et al. 2001). Unlike the globally consistent CO_2 increase, the increase in O_3 and other pollutants are highly location specific.

O_3 affects leaf gas exchange (Cojocariu et al. 2005). In localized studies, higher levels of O_3 and other pollutants were also associated with insect-related disturbances (Jones et al., 2004). O_3 was also found to interact with frost (Oksanen et al. 2005), increasing the negative effects of frost on pigment loss and stomatal conductance. As indicated in the previous section, integrating O_3 responses with CO_2, temperature, and precipitation changes within models, yields alternative productivity predictions (Hanson et al. 2005). There is no doubt that the increase in atmospheric O_3 will modify the response of forest to elevated CO_2, temperature, precipitation, and radiation but the nature of that response is unclear.

N deposition N deposition in the eastern U.S. can reach 10 kg N/ha/yr and is estimated to have increased 10 to 20 times above pre-industrial levels. Depositions of 9 kg N/ha/yr have been reported in California. One kg N/ha/yr is a common rate of deposition in the inland Northwest of North America, while areas in Europe can see deposition levels as high as 50 kg N/ha/yr (Galloway et al. 2004). In the Great Smoky Mountains National Park of the USA, it is estimated that of the 28 kg N/ha/yr deposited from the atmosphere at the high elevations, approximately 10 to 20 kg N/ha/yr are lost in runoff. In the early 1990s, reactive N creation by anthropogenic activities was estimated at 156 TgN/yr globally (Galloway et al. 2004).

The increase in atmospheric N deposition onto forest soils may be an important contribution to carbon balance of forests. Atmospheric depositions of N are thought likely to enhance growth for many temperate coniferous forests sites where N is

considered to be the most commonly limiting nutrient (Breymeyer et al. 1997). However, a saturation of N may occur, as per Verburg's (2005) findings, contributing or even accelerating the leaching of other essential nutrients such as calcium, magnesium, and potassium. To date, experiments indicate that increases in N increase C sequestration (e.g., Adams et al. 2005, Hagedorn et al. 2005), but that the effects of N deposition are modulated by the biochemical characteristics of the dominant litter (Gallo et al. 2005). Not only are atmospheric N deposition levels increasing, but temperature increases also affect soil nitrogen content and availability. For certain regions, Körner (2000) speculates that the consequences of climatic changes and soluble N deposition are likely to be greater than CO_2 effects on the carbon balance of vegetation, and his prediction seems to befit the response of northern European forests to higher N deposition found in this review. Nowak et al.'s (2004) analysis of FACE site observations showed increased productivity with increasing available N. C/N ratios are important in the estimation of carbon in soils, and hence changes in C/N ratios as a result of N deposition can greatly affect NBP estimates.

The contribution of N, much like O_3, is not completely decipherable from individual effects of temperature, precipitation, radiation, CO_2 or from its own interactions with other pollutants. All these interacting gases from the increase in pollution since the 1950s add to the already self-confounding climatic and photosynthetic role of CO_2, rendering the possible interactions and effects seemingly infinite and undecipherable. Multiple-factor analyses such as Hanson et al. (2005) and Verburg (2005) may lead to clearer answers; however, none of the changes in polluting gas concentrations is occurring independently and experiments isolating the independent effect of one may not give us much insight into the effects of their co-occurrence. In an attempt to incorporate all known mechanistic interactions of CO_2 and stand age into a forest growth model, Kirschbaum (2005) concluded that there are no simple and generally valid interactions between rising levels of CO_2 and forest age, and cautions that this interaction must be further researched before any conclusions regarding the effects of CO_2 on forests may be made. Not only are the effects of CO_2 on growth and photosynthesis at various stages of tree and stand development not clear, they also are not often incorporated in our models

and experiments and neither are the known effects of other pollutants. The effects of these and other multiple, interacting environmental factors must be elucidated through further research and modelling (Norby and Luo 2004).

Biogeography Synergistic interactions among factors will occur and so will species adaptation, both changing the NPP and carbon balance of a given site. Plants adapt to changes in environmental conditions. A good example of such adaptation is found in a review of published studies from the Luquillo Mountains of eastern Puerto Rico. Productivity in that study declined while stem density increased with elevation, as is typical of other montane forests with the exception of a mid-elevation floodplain palm stand with high levels of productivity (Waide et al. 1998). High productivity in the palm-dominated floodplain forest is apparently explained by specific adaptations of palms to the conditions found in the floodplains (Frangi and Lugo 1985). Another adaptation became apparent with the comparison of trees of the same species growing in different environments, where trees in warm dry sites had a lower leaf area to sapwood ratio than those in cool moist sites (DeLucia et al. 1994, Mencuccini and Grace 1994, DeLucia et al. 2000, Maherali and DeLucia 2000). In this case, changes in leaf to sapwood areas and in hydraulic conductivity seem to act together to maintain a similar water potential gradient (DeLucia et al. 2000). Differing growth responses of species to drought at low and high elevation extremes have also been reported (Adams and Kolb 2004). These few examples of studies of changing traits within a species under varying environmental conditions suggest that trees may be changing with the changing climatic conditions.

Genetic traits may also be changing; however, much of the genetic diversity in forests is within rather than among populations (Hamrick, 2004). Hence, adaptations to climate changes may not be apparent on the landscape by the loss of whole populations but may be happening in specific traits of individual trees (Hamrick 2004, Savolainen et al. 2004). Genetic selection of traits happens at a slow pace (Savolainen et al. 2004), and hence, the longevity of trees would not allow us to see changes in physiological or genetic traits over the past 55 years of climate change (Hamrick 2004). Large changes in species composition that would affect productivity may therefore take a long time to be visible

across many of our landscapes (Iverson and Prasad 2002). Other processes than climate change may be causal to observed changes. For example, changes in lodgepole pine (*Pinus contorta*) distributions were observed by Johnstone and Chapin (2003) in the Yukon Territory of Canada and this phenomena was attributed to climate change. However, Bergeron et al. (2004) caution that the northerly migration of lodgepole pine may not entirely be a climatic phenomenon, but rather a vegetation stabilization process still underway following the Holocene period.

Be it changes or losses in species traits, or species composition changes due to disturbances or other phenomena, changes are reported and affect the interpretation of, and contribution to productivity responses to recent climate changes. For now, the time scale and the reversibility of future and present ecological changes as a result of global warming remain unclear (Maslin 2005).

Measurement limitations Limits of estimation methods of carbon accumulation and forest stand dynamics also hinder progress in accurately depicting climate effects on forest productivity. Tree bole growth is considered a sensitive indicator of total tree carbon balance because of its low priority for carbon allocation (Ryan et al. 1996) and may be a good driver for productivity estimates, but even above-ground carbon accumulation can vary drastically over the development of a stand with accumulation rates increasing exponentially as trees increase in size and additional trees establish, and it can also be highly variable (Hicke et al. 2004, Lagergen et al. in review). In an attempt to estimate the carbon budget of Scots Pine forest in the Netherlands, Schelhaas et al. (2004) assessed the NEE of Scots pine using two different methods and found important discrepancies between the estimates. Using forest inventories, the carbon sinks of these forests were estimated at 202 g C/m^2/year with a confidence interval of 138 to 271 g C/m^2/year, compared to 295 g C/m^2/year using the eddy covariance method, with confidence intervals of 224-366 g C/m^2/year. This last study discredits measurement techniques which seem to lead to imprecise yield estimates or biased measurements. However, Krankina (2004), showed a high degree of accordance between field and satellite estimates of both total live forest biomass and mean C sink (272 and 269 TgC,

and 0.36 and 0.34 MgC/ha/year respectively) for a site near St. Petersbourg in Russia. Schelhaas et al.'s (2004) findings may leave the actual amounts of increased productivity on uncertain footing, but the overall changes for temperate forests are still positive. Schmitz et al. (2003) urge caution in the use of either of the prominent methods to assess climate change effects, the first being empirical synthesis and modelling of species range shifts and life-cycle processes that coincide, and the second being experiments examining plant–soil interactions under simulated climate warming. Although both approaches indisputably point to changes in our ecosystems due to changing climatic conditions, Schmitz et al. (2003) maintain that both approaches often provide conservative estimates of the effects of climate change on ecosystems. Schmitz et al. (2003) underline the lack of understanding of the interplay and feedback among higher trophic levels in ecosystems (top-down processes) and speculate that these may have a larger than presently estimated effect on plant species composition and ecosystem services such as productivity.

An important distinction must be made between measures of productivity such as NPP, NEP, NBP and NEE. NPP implies an overall increase in production, a faster turnover rate, NEP and NBP are net gains in biomass at different spatial scales, while NEE is a net CO_2 flux. As per the findings of Körner et al.(2005) in their analysis of four years of data at a FACE site, an increased NPP, where the added carbon was uptaken by trees at a higher rate, does not necessarily result in a net gain in biomass. Published findings sometimes support an increase in NPP and NEP at various stages of development under our changing climate conditions and sometimes do not (Law et al. 2001). It seems that an analysis of the same data at different scales may show an increase in NPP at one scale, a decrease of NEP (adding heterotrophic respiration) at another, and an overall NBP estimate varying with seemingly random disturbance patterns. The differences between full forest sector inventory based methods (which measure NBP) and flux-tower measurements (Van Tuyla et al. 2005) suggest that the eddy-flux networks overestimate long-term sinks because they do not take into account harvesting, and hence, assess NEP as opposed to NBP (Nabuurs et al. 2003). Uncertainties in eddy-flux tower data (which are prominent in the tropics - (Clark et al. 2003)), however, have been shown to be small (<3% annually) but sensitive to how low-frequency and non-horizontal flows are treated

in their estimation. As per Cahill et al.'s (pers. comm.) conclusion after attempting to estimate carbon fluxes in temperate grasslands, it is extremely difficult to close the carbon balance in forests. Linking plot-level measurements of NPP to large-scale NBP estimates requires an estimate of disturbance rates and a precise estimate of disturbance is not easy or simple to obtain. The magnitude and sign of NEP estimates are presently affected by uncertainties in estimating above-ground NPP as a whole and at different stages of stand development, below-ground NPP and autotrophic and heterotrophic respiration estimates. Hence, the question remains of how much carbon gets taken up and stored in forests.

Land use estimates are also an unknown factor, especially at global scales. Although we mostly address changes in growth rate as opposed to total growth of forest, the precise estimation of the forested status of a piece of land is important for evaluating a change in productivity though time since estimates are often calculated as means over a large area. This problem applies particularly to satellite-based estimates of production, where land classification further confounds the mechanistic and spatial uncertainties of NPP estimates (Greer et al. 1998, Houghton et al. 1999, FAO 2000, Innes and Peterson 2001, Pacala et al. 2001, Lepers et al. 2005).

To determine current climatic responses of forests around the world will require careful annual monitoring of ecosystem performance in representative forests. A lack of reliable data for below-ground NPP and an incomplete understanding of mechanistic processes in forests, and between forest and the atmosphere, are major contributors to our inability to build reliable evidence or to agree on the evidence we do have on the impacts of climate change on forests. A main problem with experiments is that isolating one or a few factors and finding the effects of these throughout a pre-defined range of variability does not give any insight into how the systems as a whole will behave with changing climatic conditions. The use of simulation models is essential for both research and management as some societal change or preventative management may help us avoid drastic changes in world climate. In the last half-century of climate change, methodological capacities in physiological research have grown tremendously and so has our understanding of

physiological processes. Monitoring of physiological processes under climate change has only become a noteworthy issue in the latter portion of the 20th century and the growing focus on the effects of climate change combined with these advances will hopefully contribute to rapidly advancing our knowledge of forest systems.

LINKING NET PRIMARY PRODUCTION MEASUREMENTS ACROSS SCALES FOR FOREST ECOSYSTEMS IN AUSTRIA

Introduction

Forests are an integral part of the economy of many countries and an important component of the global carbon cycle. Evolving interests and technologies have brought on the measure of forest characteristics across scales. The mechanisms controlling forest characteristic variability change according to the spatial scale of analysis (Innes 1998). Processes detectable at one scale may become less apparent and have a lessened effect as one increases or decreases the spatial scale (Sheriff et al. 1995). The variation of a measured characteristic results from the expression of an array of processes. The processes that are in focus at one scale of measurement are not necessarily detectable at another, but still contribute to overall variability. Which processes become visible at a specific scale is site-dependent. There are published examples of key processes being detectable at one scale and not at another. Holman and Peterson (2006) analyzed growth patterns at multiple scales (plot, forest type, watershed, and subregion). They found that inter-decadal climate patterns did influence growth at the plot level. In a study of 104 tropical forest plots, Malhi et al. (2004) found no relationship between wood production and the three main drivers of primary production: radiation, precipitation, and temperature. These findings do not imply that inter-decadal climate patterns have no effect on growth at the plot level or that the known drivers of primary production are irrelevant to wood production, but show that these were not the dominant or most apparent drivers of growth variability at these respective observation scales.

Forest resources are commonly addressed by forest inventories based on point sampling methods for assessing volume production. However, new methods such as satellite or radar technologies may be seen as support for terrestrial field survey to assess productivity and may also provide a way to link the bottom-up approaches, such as surveys, to the top-down understanding of forests that remote sensing methods provide.

The combination of different methods and data sources is one of the challenging research fields in large scale productivity assessment studies.

Direct measurements of forest NPP are quasi-impossible (Clark et al. 2001). NPP must therefore be evaluated by indirect methods, even for on-site estimates. However, the importance of accurate NPP estimates cannot be overemphasized. NPP estimates enter into the global carbon budget (Lucht et al. 2002, Nemani et al. 2003), and large-scale patterns in food and fiber production (Running et al. 2004, Turner et al. 2005). NPP estimates play a role in decision making processes involving forest health, carbon sequestration, and ecosystem management (Chen et al. 1999, Harmon and Marks 2002, Bascietto et al. 2004, Beedlow et al. 2004, Briceño-Elizondo et al. 2004, Jackson and Schlesinger 2004, Shibata et al. 2005). They are also an integrated part of our efforts in understanding physiological processes in forests, defining their local contribution to larger carbon budgets, and understanding the effects of climate change on individual forests and on the biome as a whole (Goulden et al. 2006, Bergeron et al. 2007, Friend et al. 2007, Reichstein et al. 2007, Richardson et al. 2007, Sefcik et al. 2007). Reliable and globally available site-level NPP estimates would be a large contributor to decisions leading to sustainable land use decisions and forest management, forest health, and climate change effects monitoring, and would support monitoring of carbon sequestration amid forest management practices. We presently have satellite NPP estimates, but widespread site-level estimates require large amounts of resources and are therefore sporadically available. The relationship between site-level NPP estimates and satellite estimates is, as yet, not clearly defined and like many biome characteristics, the scale at which we measure NPP can have a dramatic effect on the picture or knowledge our data reveals (Levin 1992, Rastetter et al. 1992, Davidson and Wang 2004, Urban 2005).

In this paper we compare Net Primary Production (NPP) estimates at four different spatial scales using 166 sites across Austria. We compare satellite-based NPP estimates from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor on NASA's Earth Observation Satellite (EOS), estimates from the process-based model Biome-BGC (Running and Hunt 1993) (BGC), and estimates calculated using forest-inventory data

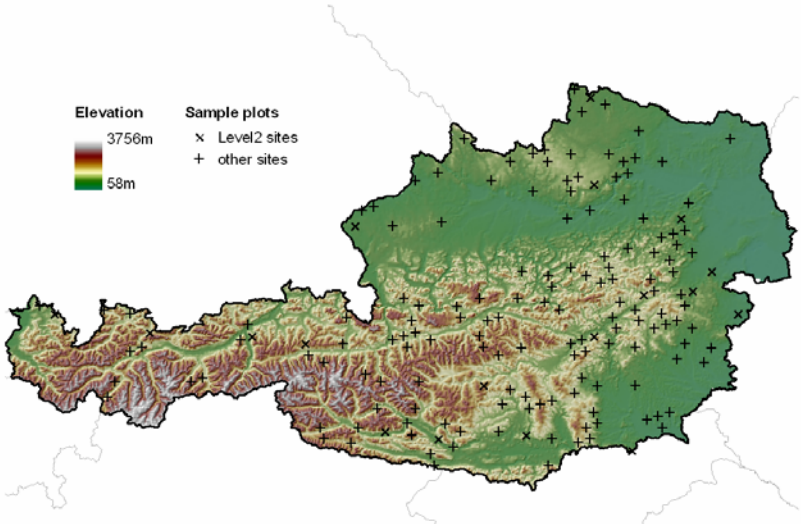
and Biomass Expansion Factors (BEF). The goal of this paper is to use this unique opportunity to explore how characteristics, and therefore the processes that drive them, change, express themselves, and relate across scales. By analyzing the measurement of the same variable across scales and using published examples of scaling studies, we show how measurements relate across scales. We also show that although different driving processes explain their individual variability, they still have common drivers at specific observation scales.

Methods and Data

Sites

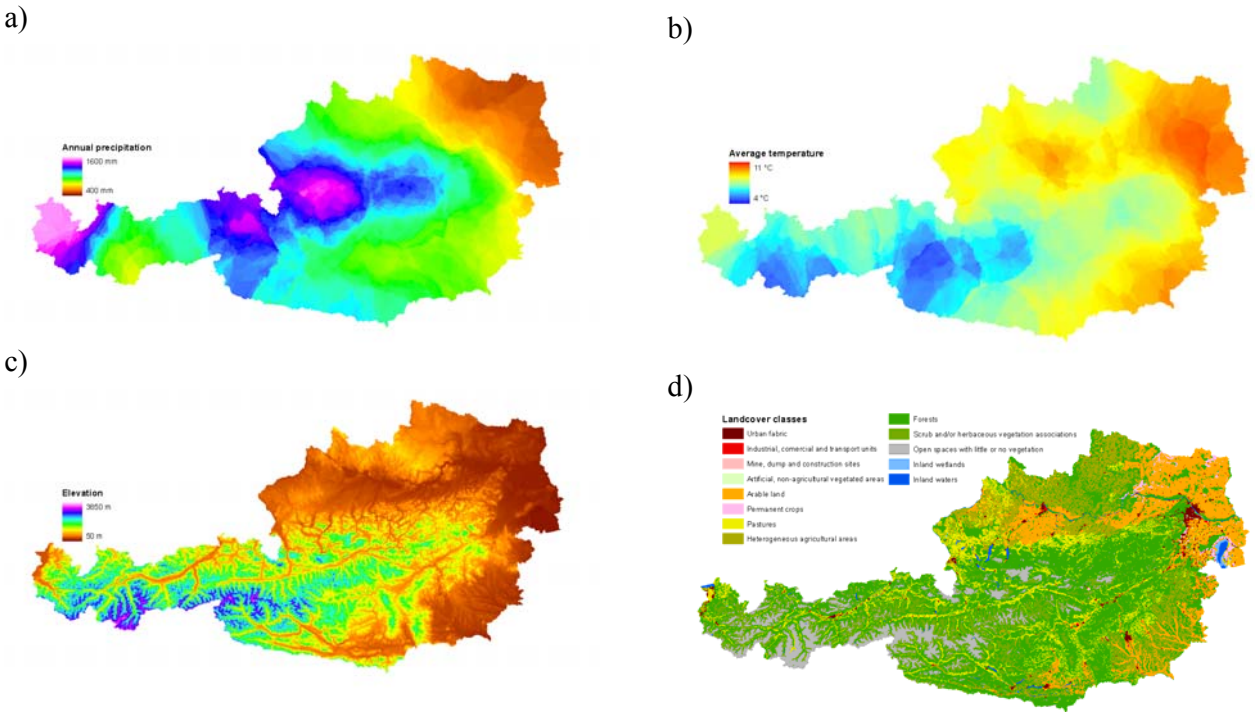
We obtained MODIS, BGC and BEF NPP estimates for 166 forested sites across Austria (Figure 2.1). To avoid biasing our analyses, only latitude, longitude and site names were used to retrieve satellite NPP estimates for each site, hence, satellite estimates are independent of forest inventory or ecophysiological data-based estimates.

Figure 2.1 Site locations of NPP estimates for comparison of ground, modelled and satellite-based NPP estimates (for 166 plots across Austria).



Austria has a very distinct combination of topography with the Alps and site history through forest management; however, primary production drivers (temperature, precipitation and light) are not as variable as they are in other places in the world. Figure 2.2 gives an over-view of Austria's primary drivers. Austria has a 7 ºC range in average temperatures and total annual precipitation levels

Figure 2.2 Maps of annual precipitation (a), average temperatures (b), elevation (c) and land cover (d) for Austria.



ranges from 400-1600 mm per year which also indicates that clouds do not significantly alter the amount of light reaching the land surface.

Estimates

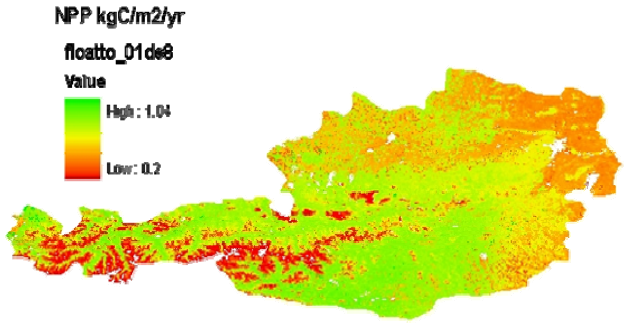
With the increasingly broad community of scientists and policy makers interested in carbon estimates, carbon measurements require a clear definition (Chapin et al. 2006). NPP is a carbon flux defined as the photosynthesis of the system minus the respiration of primary producers (Chapin et al. 2006). It is the accumulation of carbon in the vegetation over a specified time period. Our selected approaches to NPP estimation capture slightly different components of the carbon flux. Satellites and modelled NPP estimates calculate Gross Primary Production (GPP) and then subtract plant respiration to give total site NPP. BEF gives total tree biomass from tree diameter, height and age from which we estimated carbon changes from these total site biomass estimates. Contributions from understory vegetation in MODIS are part of the overall reflectance, while BGC does not distinguish between over- and understory vegetation and understory contributions are not included in BEF. Because it is based on tree measurements, BEF subsumes the effects of

age and disturbance but does not integrate immediate climate effects. BGC does respond to climate but does not account for the effects of age and disturbance on growth. Being derived from satellite reflectance, MODIS captures the effects of climate and disturbance but cannot account for local effects of site properties.

Each of these estimates has proven useful in their respective fields. BEF was developed to obtain biomass and carbon estimates from inventory data (Lehtonen et al. 2004, Van Camp et al. 2004, Jalkanen et al. 2005, Vande Walle et al. 2005, Briceno-Elizondo et al. 2006), whereas BGC and MODIS productivity estimates have been used in countless applications and ecological queries (Bernier et al. 1999, Hoff et al. 2002, Churkina et al. 2003, Pietsch et al. 2003, Turner et al. 2003, 2004, Bond-Lamberty et al. 2005, Leuning et al. 2005, Pietsch et al. 2005, Xiao et al. 2005, Goulden et al. 2006, Waring et al. 2006b). In the present study, all estimates were calculated on an annual (yr) and per hectare (ha) basis and span from 2000 to 2005 inclusively. Each of the three NPP estimates (MODIS, BGC and BEF) were averaged over the six year period for each site before comparisons were made. Comparing these averages was the main focus of our analysis. The reasoning behind averaging NPP estimates over six years stems from the perceptible change in forests from one individual year to the next. Height and diameter measurements, like those used for our BEF estimates, generally show very little to no change from year to year but show substantial changes over a six year period. Therefore the averaging was necessary if a cross-scale analysis was to be performed.

Satellite NPP estimates are now available for most of the vegetated surface of the planet. Figure 2.3 shows averaged MODIS NPP estimate over 2000-2005 for Austria. We retrieved annual NPP estimates at 1 km resolution from MODIS, for each of our 166 sites. The MODIS

Figure 2.3. MODIS 1 km NPP estimates averaged between 2000-2005 for Austria.



NPP algorithm developed by the Numerical Terradynamic Simulation Group (NTSG) at the University of Montana (Running et al. 2004) (http://www.ntsg.umt.edu/) is based on three main theoretical bases: (1) NPP is directly related to absorbed solar radiation; (2) a connection exists between absorbed solar energy and satellite-derived spectral indices of vegetation; and (3) there are biophysical reasons why the actual conversion efficiency of absorbed solar energy may be reduced below the theoretical potential value. Details of the algorithm can be found in Running et al. (2004), hence, we only present a brief description here. MODIS annual NPP estimates are derived from daily Gross Primary Production (GPP) estimates. The algorithm used to estimate GPP is based on Monteith's work (1972, 1977) relating gross photosynthesis to the amount of photosynthetically active radiation (PAR) absorbed by biomass through a radiation use conversion term (ε) which is dependent on vegetation type defined by land classification. Multipliers reduce the conversion efficiency (ε) when either cold or vapour pressure deficit (VPD) constrain plant function. A MODIS GPP estimate requires the ε term, meteorological data (solar radiation, temperature and VPD) and estimates of the fraction of incident PAR that is absorbed by the canopy (fPAR). GPP estimates are used to calculate daily net photosynthesis. Annual NPP is the sum of daily net photosynthesis minus respiration costs. Respiration costs are estimated through LAI. Both LAI and fPAR are obtained directly from a structural land cover map and atmospherically corrected surface reflectances at 1-km resolution from MODIS spectral bands as well as from information on viewing and illumination angles (Mynemi et al. 2002).

GPP, fPAR and LAI all require meteorological data as input. When retrieving MODIS NPP estimates, the meteorological data are retrieved from NASA's Global Modeling and Assimilation Office (GMAO). However, MODIS GPP productivity estimates have shown to be very sensitive to meteorological inputs (Zhao and Running 2006), hence, the developers of the algorithm (NTSG) have made an in-house modification to the algorithm which permits the use of local meteorological data. In a preliminary step to our analyses, we used both the MODIS NPP estimates employing GMAO meteorological data (*modis*) as well as the modified algorithm with local meteorological data (*local*). To ensure that we can quantify the variation in NPP due to the algorithm modification, we also

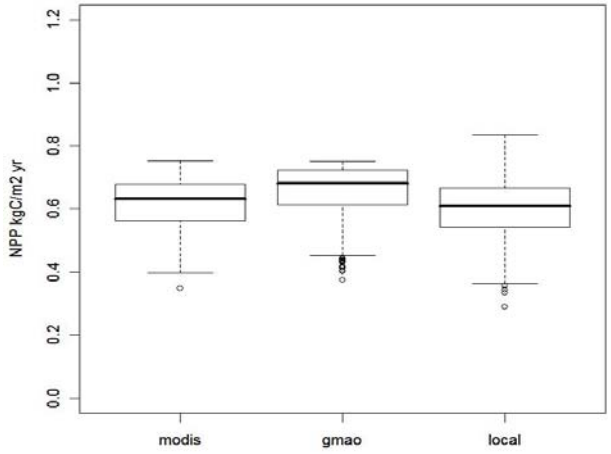
calculated NPP estimates using GMAO meteorological data and the modified algorithm (*gmao*) (Table 1.). All of these estimates originate from the same algorithm and vary little amongst themselves. The little variation they show is due to meteorological inputs and in the small modification to the algorithm, which only differs in the calculations of averages. By using the three estimates (*modis*, *gmao* and *local*) we were able to identify the part of the variation in our satellite estimates that is due to meteorological inputs and algorithm differences. Among the satellite estimates, *gmao* was slightly higher than *modis* and *local* on average, and *modis* and *local* were comparable (Figure 2.4). *Gmao* uses the same meteorological data as the *modis* and the same algorithm as *local* (Table 1). These are the only differences in these estimates. Of the small average difference between the satellite estimates (0.05 kgC/m2/yr) about 80% is due to the algorithm, while about 20% is due to the meteorological data. In our main analyses, we compare the satellite estimate that uses local meteorological data to BGC and BEF estimates for all analyses except our factor analyses, where all three satellite estimates were needed to ensure conversion.

Table 2.1 Satellite estimates of NPP by meteorological input and algorithm type.

	Meteorological data source	
	GMAO	**Local**
Original algorithm	*modis*	n/a
Modified algorithm	*gmao*	*local*

The 1-km MODIS data has been shown to have about ± 100 m geolocation uncertainties (Tan et al. 2006). Due to these georeferencing constraints, and to ensure pixel-to-site coherence, an average kgC/m^2/yr was obtained for a 3 km X 3 km area around each the latitude and longitude position of each site. Each of these nine pixels has an associated land classification (MOD12). The pixel classification determines the value of physiological parameters, such

Figure 2.4 Comparison of satellite NPP estimates for 166 sites across Austria. Average values: *modis* 0.61, *gmao* 0.65 and *local* 0.59.



as ε, through a Biome Parameter Look-Up Table (BPLUT). In theory, the central pixel has the highest likelihood of containing the site latitude and longitude but the selection of nine pixels ensures that the site coordinates are included in the pixels. Of the 15 land classes used in MODIS, six are potentially forested. Each of the nine pixels retrieved for an individual site potentially has a different land classification. For each site, only one land classification was selected and only pixels falling in the selected land class were used to calculate an average for that site. Strict *a priori* rules were followed to determine which land class was used as the basis for calculating an average for each site. First, only forested land classifications were permitted since we know all sites are forested. Second, for each site, the site name, when indicative of the species composition, was used to select a classification. For example, the site names "picea_29" may have six pixels classified as "evergreen needle-leaf forest", one pixel classified as "deciduous broadleaf forest" and two pixels classified as "water". In this case, only NPP estimates from the six pixels classified as "evergreen needle-leaf forest" would be used to calculate an average for the site "picea_29", as from the name we deduced that this was a spruce dominated forest (*Picea abies*). Similar rules were developed for all names. For sites where the dominant tree species could not be deciphered from the name, the most frequent forest land class amongst the nine pixels was selected.

Ecophysiological Estimates Modelled NPP estimates were obtained from simulations of the biogeochemical process model Biome-BGC (Running and Gower 1991, Thornton 1998, Thornton et al. 2002). Biome-BGC is a member of a class of ecosystem process models sometimes referred to as green-sponge models because it treats the landscape canopy as a single layer of leaves of a given thickness and is neither individual-based nor species-specific but uses site conditions, vegetation physiological characteristics and meteorological data to simulate ecosystem changes through time. We used version 4.1.1 with a model parameterization adapted to central European forests developed by Pietsch *et al*. (2005), adapted hydrology (Pietsch et al. 2003) and improved self-initialization (Pietsch and Hasenauer 2006). Daily records of minimum and maximum temperature, precipitation, vapor pressure deficit and incident short wave radiation, needed for running the model, were generated using DAYMET a climate interpolation model (Thornton et al.

1997) recently adapted and validated for Austrian conditions (Hasenauer et al. 2003) and local meteorological tower data. The meteorological data are the same as those used in our satellite estimates.

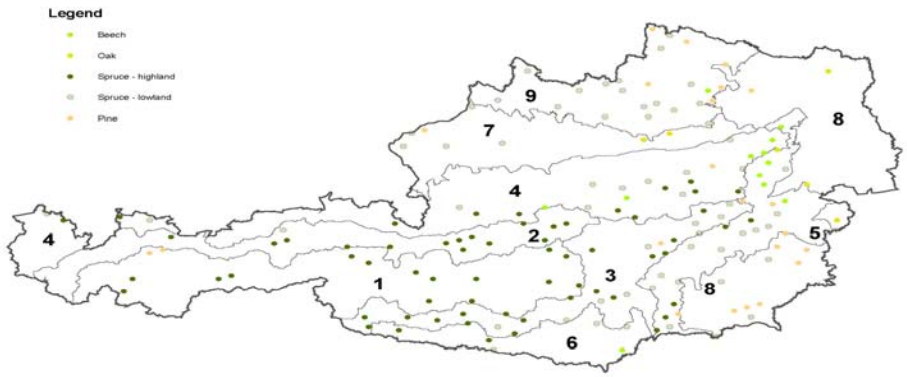
Inventory-Based Estimates Biomass Expansion Factors (BEF) were applied to individual tree heights, diameters, species and plot-level ages to obtain our final NPP estimate. Vande Walle *et al*. (2005) equations were used for beech, oak and other broadleaved species. whereas Lehtonen *et al*. (2004) equations were used for Scots pine, spruce, and other conifer species. Individual tree volumes were calculated from diameter and height measurements. Volumes were linearly extrapolated for missing years, and then used in the BEF equations to estimate total tree carbon. Trees were summed per plot, and inter-annual plot level differences yielded NPP estimates for the plot. Age, which was used in the Lehtonen equations, was only available at the plot-level and not for individual trees.

Analyses

Analyses were first performed on the 166 individual sites. Sites were subsequently grouped to further explore the link between our estimates across spatial scales. Nine previously defined main growth districts (Figure 2.5) and 22 detailed growth districts for Austria (Kilian et al. 1994) were the basis for grouping the sites. In addition to the main and detailed growth districts, we merged some of the main growth districts to obtain five larger regions, for a total of four spatial scales (plot-level, detailed, main, and merged growth districts). At each aggregation above plot-level, sites were average over each defined regions by estimation method (BEF, BGC, MODIS).

According to Milner *et al*. (1996), forest inventory yield classes are a measure of potential productivity and should roughly correspond to our NPP. Hence, we compared our productivity estimates with this well known measure of potential productivity to provide an indication of the plausibility of our NPP estimates. Yield classes are an extension of site index measurements which have long been known as a crude measure of *potential* site productivity (Sammi 1965). Site index and derived measurements of

Figure 2.5 Main growth districts as defined by Kilian *et al*., (1994). These main districts growth districts are an example of the regions used to group sites to provide another spatial analysis level. Three groupings were used, detailed growth districts, main growth districts (shown) and merged growth districts.



potential productivity are still widely use because of their simplicity (height of best tree) and ease of measurement. We then compared absolute values (means and Coefficient of Variation (CV)) across all sites between estimates and finally, we calculated Pearson's correlation coefficient (Zar 1996) as a measure of the linear association between estimate pairs for all 166 sites. Correlations between individual year estimates were also calculated to verify whether the data contained any temporal anomalies. For each of our three groupings beyond plot-level (detailed, main and merged growth districts) we again compared the linear association between methods with Pearson's correlation coefficient. A confirmatory factor analysis (Dillon and Goldstein 1984) of the NPP estimates was also completed in an attempt to quantify what our estimates have in common across our 166 plots and for each of our three groupings. All analyzes and graphs were produced using R version 2.5 (2007-04-23).

Results

In Figure 2.6, we plotted our NPP estimates against Austrian yield classes. Although yield classes are a measure of potential, rather than actual, productivity they should still show similar trends as NPP. All three estimates have a significant positive linear slope along increasing yield classes (slopes $\neq$ 0). MODIS exhibits the weakest trend ($r^2 = 0.01$, p-value = 0.0969); BEF, the best ($r^2 = 0.21$, p-value <0.001) and BGC has an $r^2 = 0.13$

Figure 2.6 Satellite, modelled and inventory-based NPP estimates for 166 sites across Austria plotted against Austrian yield classes which represent the average annual potential increment rates/ha on a 100-year rotation.

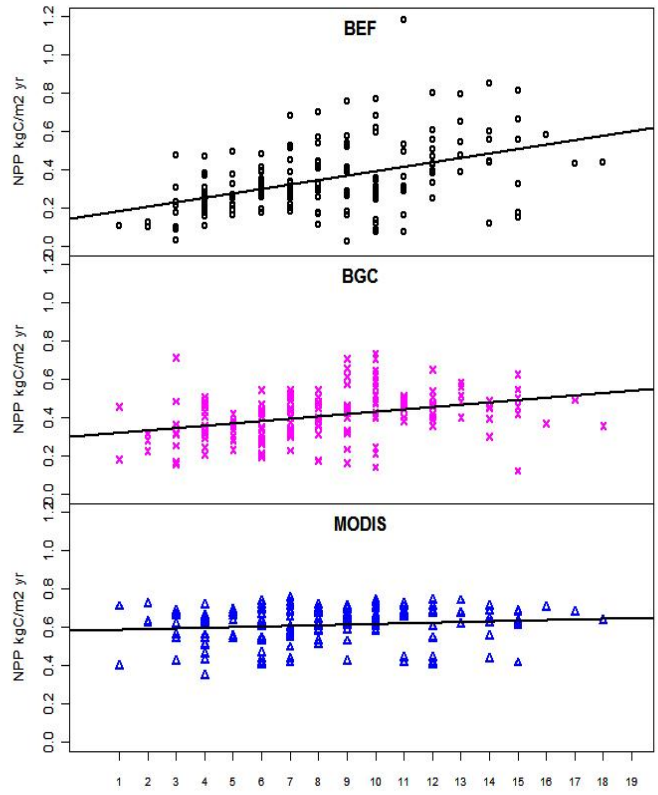
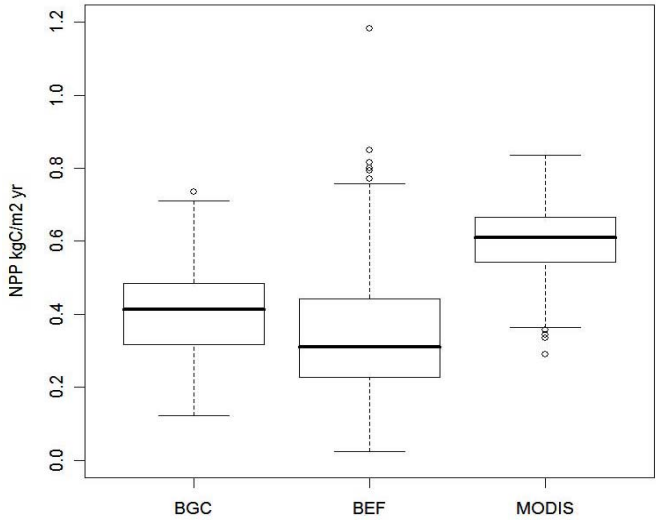


Figure 2.7 Average and range of MODIS, Biome-BGC and inventory-based Biomass Expansion Factor NPP estimates for 166 sites across Austria.



with a p-value <0.001. All our estimates fall within the range of plausible NPP values for forested sites in Austria.

Comparing average NPPs across all sites (Figure 2.7), satellite estimates were higher than BGC and BGC were higher than BEF. BEF shows the highest CV (0.52), with NPP ranging from 1.182 and 0.024 kgC/m^2/yr. BGC produced the second most variable estimates (CV = 0.3), and MODIS the least (CV = 0.18). Estimates from satellite methods (MODIS) were on average about 30% higher than ground based estimates (BGC, BEF) with average values of 0.59 for MODIS, and 0.40 and 0.34 for BGC and BEF respectively. Mean and CV rankings did not change in yearly comparisons (BEF>BGC>MODIS). We found the year 2003, a severe drought year in Central Europe (Reichstein et al. 2007), to be notably more variable and less productive on average but only

for the satellite estimates (Figure 2.8). For BEF and BGC estimates, 2003 was not notably different than any other year in the time-span.

Figure 2.8 Plots of yearly Coefficient of Variation and Average NPP estimates for MODIS, Biome-BGC, and inventory-based Biomass Expansion Factor for 166 sites across Austria. The red circle highlights the 2003 satellite estimates, a year of severe drought in central Europe.

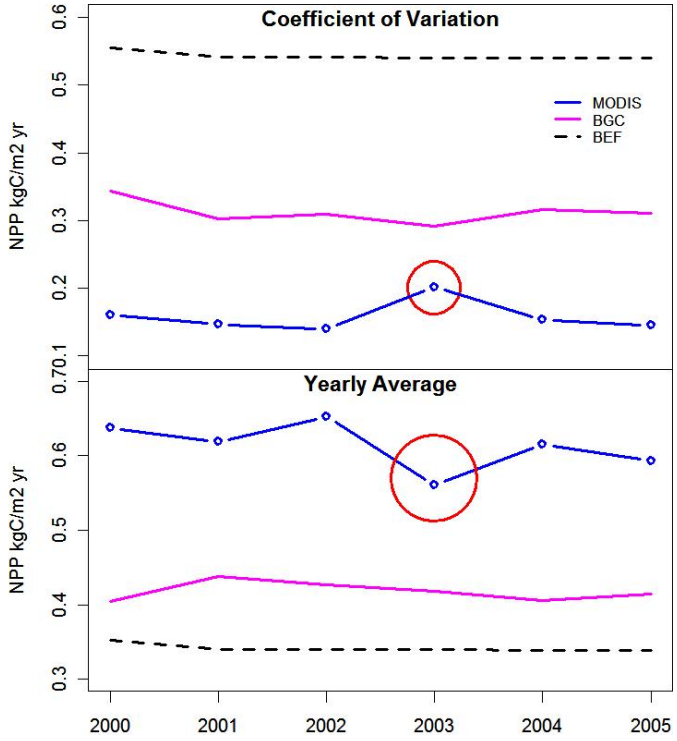


Table 2.2 summarizes all correlations between six-year averaged estimates for the 166 sites. Prior to grouping, only BEF and BGC showed any notable correlation (r = 0.35). Comparison of estimates at the three different growth district levels dramatically improved correlation coefficients for all comparison pairs. BGC had the highest correlation with MODIS at the main growth district level (nine districts for Austria) and no correlation at the merged growth district level. BEF had its highest with MODIS at the merged growth district level and also did well at the main growth districts (nine) with satellite estimates. BEF and BGC maintained their correlation at all grouping levels but did much better at the main growth districts level (nine district) and at the detailed growth district levels (21 districts) than at the merged district (five district) or at the individual plot level (166 plots).

Table 2.2 Correlation coefficients for pairwise comparisons of NPP estimates.

	N	BGC Vs MODIS	BEF Vs MODIS	BGC Vs BEF
Plot-level	166	0	-0.03	0.35
Grouped by detailed growth districts	21	0.31	0.20	0.60
Grouped by main growth districts	9	0.61	0.55	0.82
Grouped by merged growth districts	5	0.02	0.78	0.36

The final analysis we completed on our NPP estimates was a confirmatory factor analysis. A factor analysis is similar to a Principal Component Analysis (PCA). Both are data reduction techniques that identify the largest variation in data space, followed by the second largest orthogonal variation and so on. PCA does so for the total variation in the data space while factor analysis does so only for the *common* variation in the data space. Focusing on the common variation only, permits us to identify underlying factors that the data sets have in common. Factor analysis lets us estimate the contribution (factor loading) of each of our data sets to a factor, and a factor can be seen as an underlying latent variable to which all data sets contribute. In our case, if we consider the actual value of NPP on a site to be non-measurable (which is a likely hypothesis since the real value for NPP in a forest is practically impossible to measure (Clark et al. 2001)), then we can consider our five estimates of NPP to be surrogate variables for actual NPP. The actual NPP of a site can therefore be considered a latent variable or latent dimension (or factor) and an analysis of the multivariate covariance character of the data can tell us how much of each surrogate variable contribute to the real underlying NPP (first factor). As previously noted, to ensure the convergence of our factor analyses we completed one factor analysis for the 166 plots across all three methods, one analysis for the plots merged into detailed growth districts (21 averages for each estimation method), and one analysis for the plots merged into main growth districts (nine averages for each estimation method), using the three initial satellite NPP estimates (*local, gmao, modis*), the BEF, and BGC data sets. Note that this should not influence the factor loadings of the BEF and BGC data sets since all three satellite estimates are very similar and therefore, contribute almost the same variance to the five-data set common variance when all estimates are put into the analysis. Our the factor analysis at the five merged growth districts level compared only the local satellite estimate with BEF and BGC to ensure convergence of the equation system. We calculated only one factor in each of the analyses. Our results are presented in Table 2.3.

Table 2.3 Factor loadings from a factor analyses between NPP estimation methods for all plots (166 sites per method), 21, nine and five growth districts in Austria.

Estimate	All plots	21 districts	9 districts	5 districts
BGC	0.08	0.58	0.59	0.36
BEF	0.02	0.28	0.56	0.99
modis	0.91	0.95	0.87	NA
gmao	1.00	1.00	0.98	NA
local	0.69	0.85	0.94	0.78

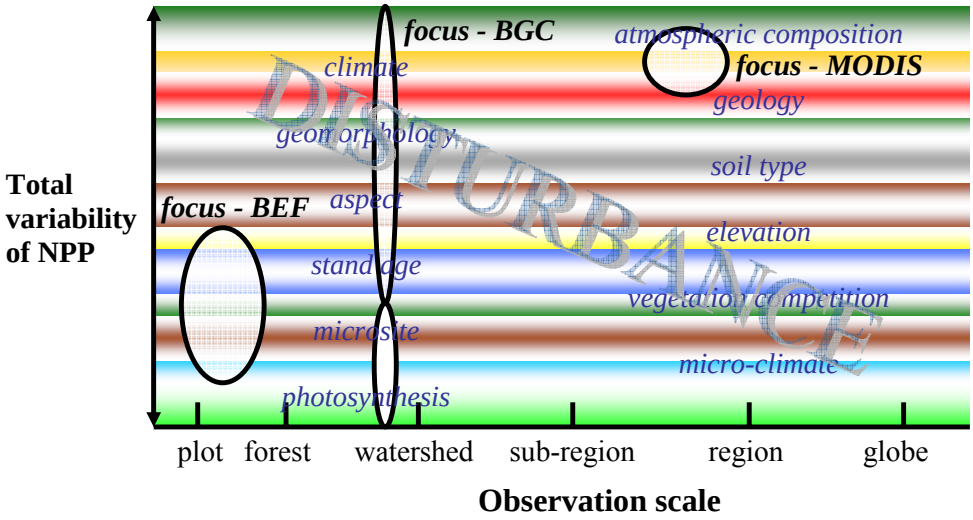
The factor analysis completed with each data set having all 166 plots showed no contribution to the common variation among estimates from BEF or BGC (first column Table 2.3). Grouping the data significantly improved the contribution to the common variation of BEF and BGC estimates. As per our correlation analysis, prior to grouping the sites, BEF and BGC estimates did not contribute to the underlying variability of the NPP estimates. They had nothing in common with the satellite estimates. Grouping the estimates spatially showed a higher contribution to the common variation, hence, a higher contribution of the underlying actual NPP for both field-based estimates. In the merged-district comparison, each data set only has five points (there are only five large districts); hence, careful interpretation of these results is in order.

Discussion

The comparison of NPP (kgC/m2/yr) estimates from two ground-based (BEF, BGC) and one satellite-driven method (MODIS) for 166 sites across Austria exhibited that the measurements had very little in common and seem to be incomparable. Our results also showed that satellite estimates were on average 30% higher than ground-based estimates. Increasing the scale revealed that the estimates had much more in common and that an optimum scaling level exists (see Tables 2.2 and 2.3).

These inconsistencies in the results at a relatively small scale versus a coherence at a larger scale is not uncommon and relates to the fact that data inputs and estimation methods applied for assessing productivity also differ by their observation scale and the underlying processes driving productivity. For example processes such as establishment, photosynthesis, respiration, growth, etc., shape the forests we observe. The observation scale changes the focus of our enquiry and hence, depending at what scale we observe the system, different dominant processes (all of which contribute to the total variability of what we see) are important (see Figure 2.9).

Figure 2.9 Conceptual summary: relationship between observational-scale, NPP variability and the processes that are in focus for each our NPP measurements MODIS, Biome-BGC, and inventory-based Biomass Expansion Factor. The observation scale (x-axis) determines the focus (ovals) and the y-axis represents the total variability on NPP. The coloured background of the figure are examples of processes and forces contributing to the total variability of NPP.



BEF estimates are based on tree measurements, hence, this estimate focuses on the effects of local stand competition on growth trends which are impossible to detect with 1 km^2 satellite estimates. The variability in tree-growth trends influenced by many local factors (competition, microsite, etc.) at this scale, are mixed in with lower resolution effects such as the influence of climate. BEF showed the highest variability since BEF "sees" more details as it uses diameter and height (tree-level measurements) to estimate NPP. BEF is, not surprisingly, the most variable of all estimates. Although BEF is statistically derived from tree measurements, it implies the contribution of non-tree components through its empirical relationship. Figure 2.9 shows the BEF estimate in the bottom left corner where all the processes contribute to its variability. However, its focus (oval) shows only a portion of that variability, that which is visible at the plot level. BGC estimates, from the Biome-BGC model which models a "green-sponge", "sees" less details than the BEF. Although BGC was not designed to model processes such inter-tree competition, it reliably simulates forests and therefore, to a certain extent, competition (Bond-Lamberty et al. 2005). However, the resolution of BGC is less than BEF. Our BGC estimates most probably capture more of the variation due to larger scale factors such as climate, as compared the BEF estimate, while the satellite estimates capture such

effects even more than the BGC. BGC does account for much of the identified processes and forces affecting the forest (hence, the narrow oval crossing all the processes involved in NPP variability in Figure 2.9) but has some generalizing features (necessary for its regional applications) that limit its comparison to system level models or field observations. Satellite estimates capture the variability due to processes of larger-scale influence, such as climate rather than those due to inter-tree competition. Hence, Figure 2.9 shows the focus (oval) of MODIS in the top right section of the variability-and-observation-scale space.

According to Figure 2.9, aggregation of BEF NPP estimates should have more in common with lower resolution observations such as our BGC and MODIS NPP estimates. Our results show exactly that: as estimates are aggregated over growth districts both the correlation and factor analyses show that the results have much more in common than when individual plots are compared. BEF had no correlation with MODIS across the 166 plots, had a correlation of 0.31 with MODIS across the 21 detailed growth districts and a correlation of 0.61 across the nine main growth districts (Table 2.2). BGC correlations with MODIS went from -0.03 to 0.20 to 0.55 from the plot-level to the detailed and main growth districts, respectively (Table 2.2). Correlations between BGC and BEF also increase with scale from 0.35 across plots, to 0.60 and 0.82 at 21- and nine-growth district scales, respectively (Table 2.2). Increased correlations identify an increase in linear association, while the increased factor loadings represent an increase in shared multi-dimensional space and a high contribution to the first factor, which represent the actual NPP, a latent variable.

Despite warnings of the misleading nature of short-term and small spatial-scale studies (Burke and Lauenroth 2002), our reasoning and published examples (Holman and Peterson 2006, Bala et al. 2007) show that these small scale observations contain useful information even for regional applications. Aggregated, they share much commonality with large scale studies; hence, they certainly contain valuable information. Besides, they remain the main operation scale for decision making and individual land-use decisions

and may contribute to the decline of whole biomes (e.g. clear-cutting in the tropical rain-forests).

The detection by satellite NPP estimates of the 2003 drought (Figure 2.8) can be partially explained by the positioning of each of our estimate in the variability/observation scale space. The variability in finer-scale estimate such as BGC and BEF focuses on processes that express themselves at finer-resolution which masks the climate-effect of a drought in a one-season time scale, in other words, there is too much noise to decipher the climate-effect in BGC and BEF. In our case this is more applicable to BGC estimates since volume estimates were linearly interpolated in BEF estimates (height and diameter measurements were not available for all years), hence, partly removing annual variability. Even if yearly height and diameters were available, the focus of BGC and BEF NPP estimates is such that it most likely will not reveal the larger-scale top-down effect of the one-year drought. They show the NPP as it is influenced by inter-tree competition and other more locally expressed processes. The variability of each estimate reflects well their individual resolution. The capability of our estimates to capture the effects of one extreme summer drought event is closely related to the carbon allocation sequence in forests as well as to the basis from which NPP is calculated in each method. Instant growth reduction was captured through increases in VPD by MODIS (Reichstein et al. 2007) while LAI remained unchanged (see Table 2.4). Changes in LAI would be necessary for BGC to detect drought and changes in shoot elongation and/or diameter increment necessary for BEF to detect drought effects, both of which would only occur in the spring following a season-long drought which was not the case in the 2003 Central European drought, where temperatures cooled by the end of the growing season

Table 2.4 Yearly averages of LAI and fPAR values used in MODIS and BGC NPP estimates for 166 sites across Austria from 2000 to 2005.

	LAI		fPAR	
Year	**MODIS**	**BGC**	**MODIS**	**BGC**
2000	6.51	4.17	0.68	0.76
2001	6.50	4.21	0.65	0.77
2002	6.54	4.26	0.65	0.76
2003	6.51	4.27	0.66	0.77
2004	6.51	4.26	0.59	0.76
2005	6.56	4.28	0.62	0.76

(Reichstein et al. 2007). Due to the sequence in tree carbon allocation a longer drought might become apparent in BGC or BEF (assuming availability of yearly values) since LAI and tree height and diameter have a lapsed expression of the effects of drought. We suspect that a multi-year drought would be more quickly apparent in LAI measurements and therefore would be detected by BGC while it would take a longer time-span to be apparent in BEF because LAI (BGC driver) would respond more quickly than diameter and height (BEF driver). Reichstein et al. (2007) saw the effect of the 2003 drought in a productivity decline across European flux towers. However, they identified the decline in both GPP and respiration, which may partly explain a less apparent response when looking at BGC NPP estimates, which are generally calculated as GPP minus respiration. Despite the identified reduced ability of MODIS estimates to detect drought stress (Turner et al. 2005), the MODIS products detected the 2003 European drought as our results show, in agreement with those of Reichstein et al. (2007), show.

Our approach also establishes the link between top-down and bottom-up modelling. Both modelling approaches rarely agree (e.g., (García 2002, IPCC 2003, Schmitz et al. 2003, Hessburg et al. 2005). In a top-down approach an overview of the system is first formulated, specifying but not detailing any first-level subsystems. Our satellite estimates of NPP are a good example of a top-down modelling approach where abstraction of processes was the key to large-scale applicability. In a bottom-up approach the individual base elements of the system are first specified in great detail. Mechanistic forest models where details of photosynthesis, respiration, water balance and conductance are modelled at a leaf-level are a good example of bottom-up models. These processes are then linked together to form larger subsystems (e.g., tree or stand). The problem with this approach is that we do not fully understand all processes in forest ecosystems. Even for the well-understood processes like photosynthesis (see Farquhar et al. (1989)), at the level of a given process (e.g., leaf, or cell) a mechanistic model might rightly be regarded as causal, with coefficients that can be derived from theory. But at a higher levels of organization (e.g., tree or stand), the theory is insufficient and we often use empirical relationships to represent the system (Mäkelä et al. 2000a). Our BEF estimates based on tree level observations, can also be seen as a bottom-up approach relative to satellite observation

but the problem encountered here is that not all trees in a region can be measured. BGC estimates are partly mechanistic since the model Biome-BGC does model processes such as photosynthesis, respiration and conductance but has scaling-up methods integrated. As the number of processes we can model and understand increases, the discrepancy between bottom-up and top-down modelling may become less. However, our analyses show that much of this discrepancy can be attributed to the focus (dark circles in Figure 2.9) of modelling approaches and that each approach provides one portion of the complete variability picture. This brings to light the possibility of mathematically linking these estimates to obtain an estimate closer to the actual NPP.

The aggregation of cross-scale measurements to set spatial scales may also be the best way to identify the scale at which top-down and bottom-up effects can be linked. The maximum commonality reveals the level at which a key cross-scale process is most apparent, in our case the main growth district level. This process may be the same as found by Holman and Peterson: the top-down influence of climate as a productivity limiting factor. They found that at larger scales (watershed and subregion), forest-type growth patterns show coherence (significant positively correlated BAI growth patterns), which implies the top-down influence of climate as a growth-limiting factor on dominant growth responses of bordering forest types. Waring *et al*. (2006a) also identified the regional rather than local levels best suited to climatic relationships.

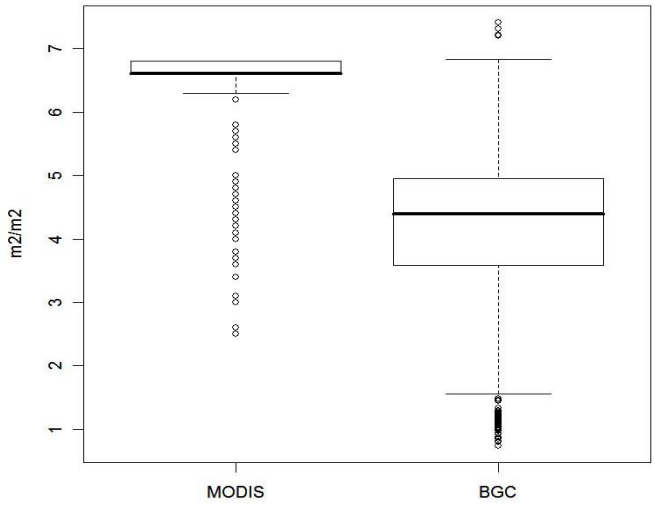
Discrepancy between Ground and Satellite Estimates

Despite their diverging approaches in estimation method, BGC and BEF estimates have a significant relationship at all comparison levels. These two ground based estimation methods are on average 30% less than the satellite based approach. Causes for discrepancies between MODIS productivity estimates and field or modelled estimates have been identified in the literature: errors in upstream MODIS products, resolution and quality of meteorological input data, biophysical attributes (BPLUT) and algorithm design (Heinsch et al. 2006, Turner et al. 2003, 2005, 2006 Zhao et al. 2005). Most large-scale approaches will carry errors due to the algorithm design because of present limitation of satellite methods to really capture the complex structure of forests and

computational limitation in handling such data. Addressing such issues is beyond the scope of the present study; hence, we recognize that some errors are present in our MODIS estimates because of algorithm issues. We limited the error contribution from meteorological data by using local meteorology for our estimates and some issues identified in the literature have been partly addressed in collection 4.8 of MODIS (Zhao et al. 2005), used in this comparison.

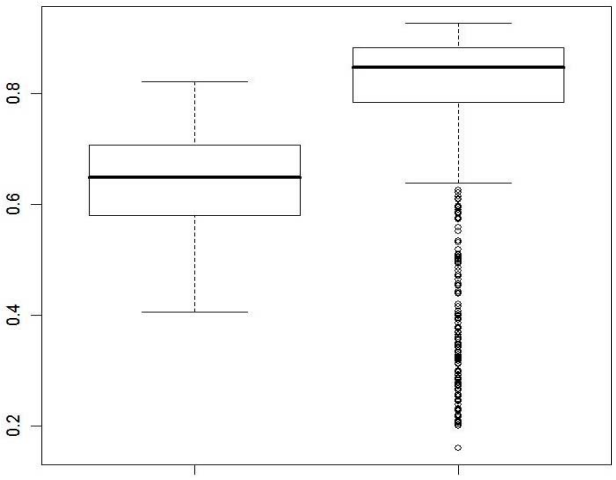
Amongst the up-stream MODIS products that affect our NPP estimates, LAI and fPAR are important contributors. LAI is directly involved in respiration estimates while fPAR determines production (GPP). Overall MODIS GPP compares well to field estimates (Heinsch et al. 2006, Martel et al. (2005), Turner et al., 2006a), but both Turner et al. (2003, 2006b) and Heinsch et al. (2006) identify an over-estimation of GPP (20-30%). Figure 2.10, Figure 2.11 and Table 2.4 show MODIS LAI and fPAR, used in our satellite estimates to be respectively higher and lower than the LAI and fPAR used in our BGC estimates. Lower fPAR values contribute to lower GPP estimation, which in turn contributes to lower NPP, but over-estimation of LAI contributes to over-estimation of respiration, which results in an under-estimation of NPP. MODIS LAI and fPAR comparisons to Biome-BGC LAI and fPAR estimates both point to an underestimation of NPP, the opposite of our findings. Without further investigation, we can only speculate that the improvements in MODIS BPLUT (Zhao et al. 2005), where land-classification-determined parameters are set, may not have been sufficient to correct the 20-30% GPP over-estimation found by Heinsch *et al*. (2006) since we also found an over-estimation in

Figure 2.10 Comparison of Biome-BGC and MODIS maximum yearly LAI values used for NPP estimation from 2000 to 2005 across 166 sites in Austria.



productivity (NPP) despite minimizing error-contribution by using local meteorological data and using the improved collection 4.8.

Figure 2.11 Comparison of Biome-BGC and from MODIS fPAR values used for NPP estimation from 2000 to 2005 across 166 sites in Austria.



One contributing factor is that MODIS measures reflectances across all nine pixels and does not distinguish between tree and understory reflectance and understory plants are spectrally brighter. Even in closed canopy stands some extra edge reflectance will be recorded due to understory vegetation increasing the overall NPP, a contribution less apparent in BGC estimates and non-existing in BEF. A major difference between MODIS and BGC that may also contribute to divergence is how they represent Light Used Efficiency (LUE) (Turner et al. 2005). MODIS bypasses the complexity of quantifying carbon, water and nitrogen cycles found in Biome-BGC by quantifying PAR absorbed by vegetation canopy through a general LUE term (ε) and restraining the conversion of that solar energy into carbon with climatological and physiological constraints. This abstraction may contribute in our case to an over-estimation of NPP in the heterogeneous landscapes and forests of Austria, but it could also contribute to an underestimation.

The range of density and species mix of our sites may have also contributed to the divergence between land-based and satellite NPP estimates. Although the version of Biome-BGC used in our estimates does incorporate forest management (Petritsch et al. 2007) it does not simulate stand <50% densities well and may not represent the actual landscape as accurately as MODIS. Further, we assumed pure stand if the proportion of the main species was greater than 2/3 of the basal area while MODIS land classification has a mixed forest classification. Most of the uncertainty in the BEFs has been related to uncertainty in the biomass and volume models applied (Lehtonen et al. 2007) and while

the equations we used were previously tested (Lehtonen et al. 2004, Vande Walle et al. 2005), they were not developed for forests of Austria. Their empirical relationships are therefore less likely to capture the reality of conditions across Austrian forests.

Stand age may also have an important influence on how ground and satellite NPP estimates diverge as stand age has been shown to be closely tied to productivity (Wirth et al. 2002, Song and Woodcock 2003, Pregitzer and Euskirchen 2004). MODIS detects all stands and all ages in the selected pixels of each site while BEF is constrained by one stand-level age and BGC by a generalized mature stand. Further, only the Lehtonen equations use age, the Vande Walle equations do not. Hence, this may contribute to lower NPP from BEF.

Heterogeneity

The maximum communality may be a good indication of where top-down and bottom-up models can be linked and an indication of the scale at which over-arching top-down influences can be monitored. This point, however, likely varies with land-base variability.

One distinguishing feature of Austrian forests is the long forest management history. Site history has been shown to be determinant in the development of forests, even at a physiological level (Ollinger et al. 2002, McIntire et al. 2005). Our sites were all under a forest management regime and showed a range of density and species mixture. Sites with different histories (McIntire et al. 2005) and different balance of primary drivers (Jolly et al. 2005) will reveal different dominant processes at the plot, sub-region and regional level than those we identified in our analysis. Sites where natural disturbances preside would also likely show a different set of dominant components of variability at the same scales (plot, sub-region and region). Hence, the nine growth district level may be the most appropriate scale to further explore how changes in climate affect Austrian forests, but may not be applicable in regions, unless the heterogeneity, both physical (topography, environmental factors, etc.) and historical, compares well to those of Austria.

Summarizing our study we conclude that by comparing NPP across scales from three distinct estimation methods, and subsequently forcing them to similar scale and repeating our comparison, we showed: 1 - that the information that we can get from one estimate is bound by its sampling scale; 2 - that despite initial disparity, these measurements are an expression of the same ecosystem flux at different scales, therefore revealing the variability of the dominant processes in their respective scale while still representing the targeted flux at that scale; and 3 – that the maximum level of commonality can be found by bringing cross-scale comparisons to similar scales and that this maximum identifies an overarching top-down process that influences all scales, such as climate. These are all dependent on site limiting factors and by site and landscape heterogeneity, and hence, will vary from one location to another.

We conclude that the best scale for the study of climate influences on forest of Austria are the nine growth districts identified by Kilian *et al*. (1994). We also caution that since NPP is a flux, resulting from the combined force of many processes, exactly which process or combination of processes link these estimates at each scale is presently undecipherable. Understanding the system and how it changes requires recognizing that processes in forests occur throughout a continuum of time and space and not in discrete instances (Levin 1992). The patterns that are unique at any range of scale will have a unique combination of time and space instances of driving processes. Information from all scales is therefore essential for a complete understanding of the system across scales. Satellite estimates of forest characteristics or patterns have helped us in the last decades to further our understanding of large scale responses of forests while field measurements show the heterogeneous fine-scale character of forests. These need to be linked and presently, there seems to be a gap in spatial scale between the 1 km^2 of MODIS and the regional BGC and BEF estimates (Justice 2006). New methods for estimating forest characteristics in that spatial scale gap (e.g., finer scale MODIS products, Light Detection and Ranging (LIDAR) or other satellite products) may permit us to further explore the relationship between measurements of the same feature of forests across scales; refine our knowledge of that feature, and of scaling issues in our heterogeneous forests.

Forest biomes have an important advantage over other biomes; in many locations there are years of inventory data. The long-term records of forest growth and yields in countries such as Austria may permit an easier link between satellite and field-based measurements. Linking inventory-based measurement, which, as we have shown, relate to satellite measurement on a regional scale, may provide the best opportunity for further understanding of the system and can permit us to identify the common scale where top-down processes (such as climate change) have the most influence in a particular region as this scale will be particular to each region (van der Molen et al. 2006). The next step may be to mathematically link these cross-scale estimates to produce the best possible NPP estimate given our current knowledge.

EFFECTS OF CLIMATE PROJECTIONS ON FORESTS OF THE US NORTHERN ROCKIES

Introduction

Documented climatic changes in the last 50 years have significantly changed the environmental conditions in which forests grow. Forests seem to have already responded to these changes (Boisvenue and Running 2006), and climatic changes are predicted to intensify in the coming years (IPCC 2007b). Projecting forest responses to increases in temperature, CO_2 concentrations, and other changes in their atmospheric environment is difficult because of the plethora of interacting factors and processes involved, all of which are the subject of much research (Hättenschwiler et al. 1997, Ellsworth et al. 2004, Nowak et al. 2004, DeLucia et al. 2005, Körner et al. 2005, Asshoff et al. 2006, Palmroth et al. 2006). Forest development stage, individual species, and localized pollution levels are just a few of the interacting determinants of responses to environmental changes that contribute to projection uncertainties. Fortunately, we have simulation models of forest ecosystem processes that can help establish a response baseline to our current climate change projections, which may enable us to avoid or at least be aware of the consequences of climate change.

The recent Intergovernmental Panel for Climate Change (IPCC) Fourth Assessment Report (AR4) synthesizes much of the latest research on climate projection and projects increases in temperatures and in the amount of precipitation at high latitudes (IPCC 2007b). Although the IPCC reports an improved understanding of precipitation patterns, Atmosphere-Ocean General Circulation Model (AOGCM) precipitation projections used in the IPCC AR4 are still highly variable. Precipitation levels play a crucial role in forest ecosystems like those in the Northern US Rockies, where ecosystems conditions range from dry to wet, with the drier forests interfacing with grassland ecosystems. The amount of water on site often drives productivity and disturbance regimes in these forests. This study establishes a baseline of responses for forests of the US Northern Rocky Mountains to changes projected by three AOGCMs using the ecosystem process-based model

Biome-BGC (Thornton 1998a). Temperature and precipitation projections from a drier (GFDL-CM2.0), a median (PCM), and a wetter AOGCM (CGM3.1(T63)), set under the atmospheric CO_2 scenario projected by the IPCC Special Report on Emission Scenarios (SRES) A1B (Nakicenovic et al. 2000), were used to project climate change effects on key forest types in the U.S. Northern Rocky Mountains.

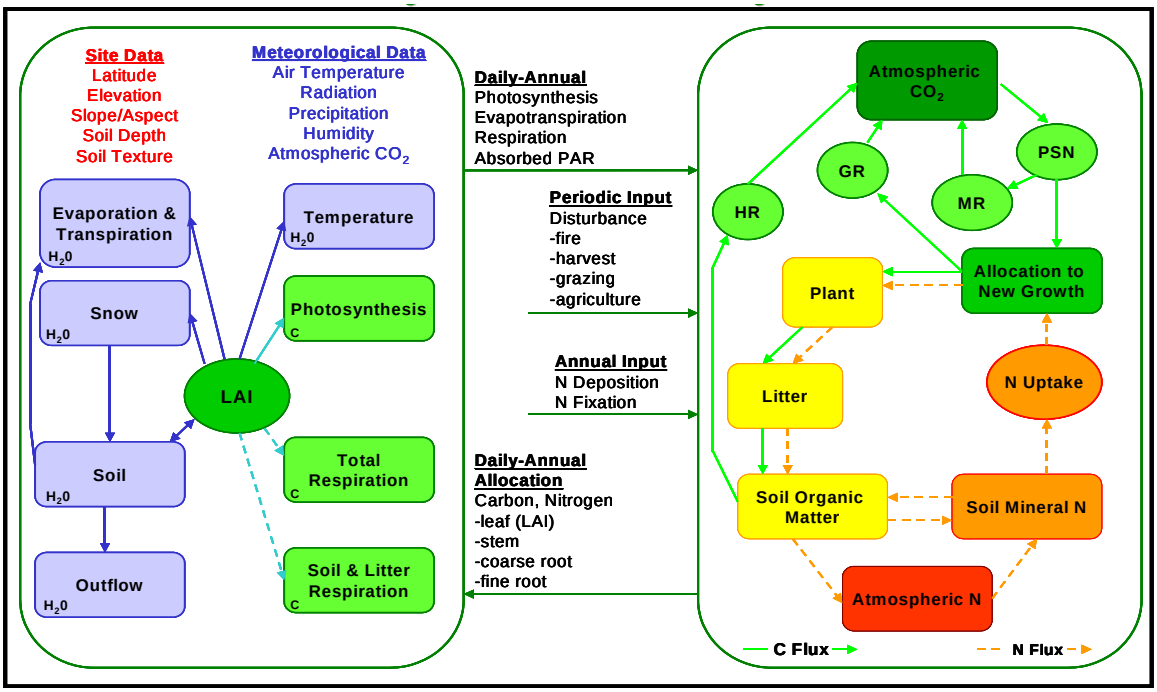
Background

Biome-BGC

Biome-BGC is a model that simulates fluxes and storage of energy, water, carbon, and nitrogen for vegetation and soil components of terrestrial ecosystems (www.ntsg.umt.edu/models/bgc). The model was originally developed for forest biomes (Running and Gower 1991) and then expanded to other biomes (Running and Hunt 1993, White et al. 2000). Biome-BGC models new leaf growth and old leaf litter fall, sunlight interception by leaves and penetration to the ground, precipitation routing to leaves and soil, snow accumulation and melting, drainage and runoff of soil water, evaporation of water from soil and wet leaves, transpiration of soil water through leaf stomata, photosynthetic fixation of carbon from ambient CO_2, uptake of nitrogen from the soil, distribution of carbon and nitrogen to growing plant parts, decomposition of fresh plant litter and old soil organic matter, and plant mortality.

Biome-BGC is a member of a class of ecosystem process models sometimes referred to as green-sponge models because it treats the landscape canopy as a single layer of leaves of a given thickness and is neither individual-based nor species-specific, but uses site conditions, vegetation physiological characteristics and meteorological data to simulate ecosystem changes through time. Biome-BGC has been extensively tested and used (Coops et al. 2001, Churkina et al. 2003, Hoff and Rambal 2003, Pietsch et al. 2003, Kimball et al. 2004, Bond-Lamberty et al. 2005, Chiesi et al. 2005, Pietsch et al. 2005) and has also been used for global applications (e.g.,Qian et al. 2006). It is driven by climate and environmental changes and was developed to respond as biomes would to the environment. Figure 3.1 shows the logic and mechanisms used in Biome-BGC.

Figure 3.1 General outline of the Biome-BGC functioning (Thornton 1998b), a process-based model.

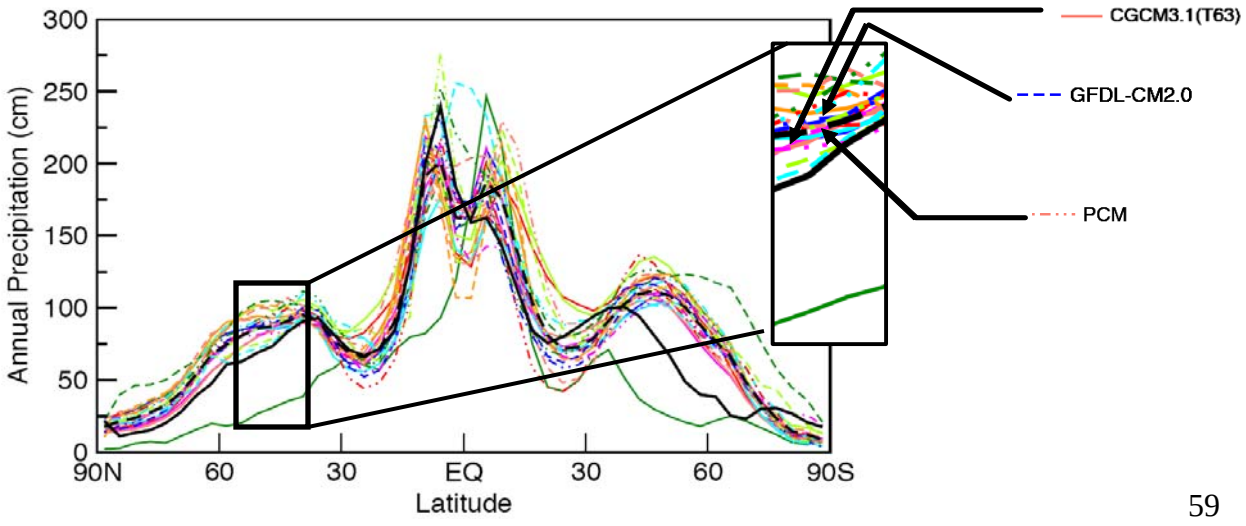


Biome-BGC requires meteorological input (air temperature, solar radiation, humidity, precipitation, and atmospheric CO_2), site information (latitude, elevation, slope, aspect, soil depth, and soil texture), and site ecophysiological information (turnover and mortality parameters, carbon allocation allometric parameters, C:N ratios, etc.) to simulate the effects of climate on forests. Weather is the most important control on vegetation processes in Biome-BGC. Flux estimates depend strongly on daily weather conditions. Model behavior over time depends on the history of these weather conditions, the climate. The model also requires a set of initial conditions from which to start a simulation. These conditions are established through a spin-up simulation which can span many thousands of years until the system reaches a steady state with respect to soil carbon. The compartment C and N values reached at this steady state are used as starting values for the simulation. Our spin-up simulations were based on actual meteorological data from 1950 to 2005 (recycled), site-specific plant ecophysiology information, and site conditions.

AOGCM

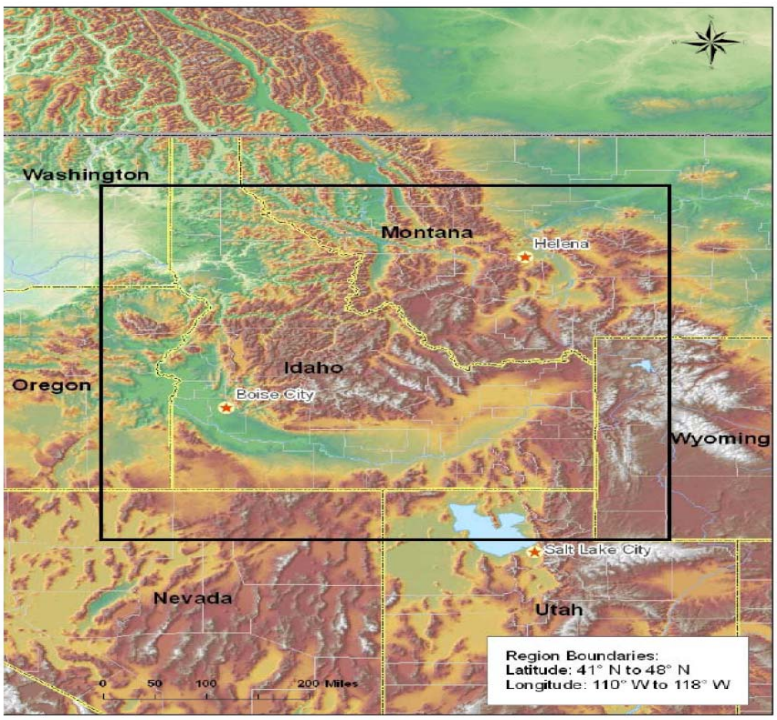
The earth system experiences a complex series of stresses to which it responds in an equally complex way. While models unavoidably simplify this reality, the increases in computing capability of recent decades has led to models, based on well-established physical principles, capable of reproducing observed features of recent climate (Randall et al. 2007) and past climate changes (Jansen et al. 2007). Atmosphere-Ocean General Circulation Models (AOGCM) remain the primary source of regional information on the range of possible future climates (Christensen et al. 2007). There is considerable confidence that AOGCMs provide credible quantitative estimates of future climate change, particularly at continental and larger scales. The precise location of boundaries between regions of robust increase and decrease remains uncertain, and this is commonly where AOGCM projections disagree (Christensen et al. 2007). Confidence in these estimates is higher for some climate variables (e.g., temperature) than for others (e.g., precipitation) (Randall et al. 2007). Because of the importance of precipitation in forests such as the ones in the US Northern Rockies region, the three selected models, of the 23 used in IPCC AR4, varied in their represented range of precipitation projections: CGM3.1(T63) model, from the Canadian Centre for Climate Modelling & Analysis, the PCM, from the National Center for Atmospheric Research (NCAR), and the GFDL-CM2.0, from the

Figure 3.2 The large pane shows observed annual-mean precipitation averaged by latitude zones from 1980-1999 (black continuous line), simulated annual-mean precipitation (coloured lines), and all model averages annual-mean precipitation (black dashed line) for the 23 models AOGCMs used in the IPCC AR4. The smaller excerpt shows the location of the three selected AOGCMs used for climate projections in this study (Wet - CGM3.1(T63), Dry - GFDL-CM2.0, Middle - PCM) amidst the 23 models for latitudes between 41 and 48 ºN, our approximate study area.



U.S. Department of Commerce/NOAA Geophysical Fluid Dynamic Laboratory. As shown in Figure 3.2, the selected models were not marginal models in the distribution of models; they were well within the distribution of models. For each model, monthly changes in values of precipitation and temperature from a base-period (years 1980-1999) to 2030, and from the base-period to 2080, were provided by NCAR for an area approximately 5.6º in latitude and longitude over the US Northern Rocky Mountains (Figure 3.3). The 2030 values represent the average change between 2020 and 2039, and the 2080 values represent the average change between 2070 and 2089. The probability distribution functions (PDF) of these three AOGCMs in a Bayesian synthesis of all AOGCMs are presented elsewhere (Tebaldi et al. 2005).

Figure 3.3 Region referred to as the US Northern Rockies for the purposes of our study. The models' grids were interpolated by NCAR to a "T42" grid, which represents the median resolution among the models contributing to the Program of Climate Models Diagnostic and Interpretation (PCMDI) archive (Tebaldi et al. 2005).



Projections from these three AOGCMs were completed under the A1B emission scenarios (Nakicenovic et al. 2000), which for our purposes provides a atmospheric CO_2 concentration for our simulation horizon. As described in the Working Group II contribution (IPCC 2007a), the A1 scenario family describes a future world of very rapid economic growth, global population that peaks in mid-century and declines thereafter, and the rapid introduction of new and more efficient technologies. Major underlying themes are convergence among

regions, capacity building, and increased cultural and social interactions, with a substantial reduction in regional differences in per capita income. The A1 scenario family develops into three groups that describe alternative directions of technological change in the energy system. The three A1 groups are distinguished by their technological emphasis: A1B describe a balance across fossil intensive and non-fossil energy sources (where balanced is defined as not relying too heavily on one particular energy source, on the assumption that similar improvement rates apply to all energy supply and end-use technologies). Figure 3.4 positions scenario A1B amongst the marker SRES scenarios.

Figure 3.4 Multi-model averages and assessed ranges for surface warming under emissions scenarios as described in the IPCC Special Report on Emissions Scenarios (SRES) (IPCC 2007b). Solid lines are multi-model global averages of surface warming (relative to 1980–1999) for the scenarios A2, A1B (our scenario) and B1, shown as continuations of the 20th century simulations. Shading denotes the ±1 standard deviation range of individual model annual averages. The orange line represents the experiment in which concentrations were held constant at year 2000 values. The grey bars at right indicate the best estimate (solid line within each bar) and the likely range assessed for the six SRES marker scenarios. The assessment of the best estimate and likely ranges in the grey bars includes the AOGCMs in the left part of the figure, as well as results from a hierarchy of independent models and observational constraints.

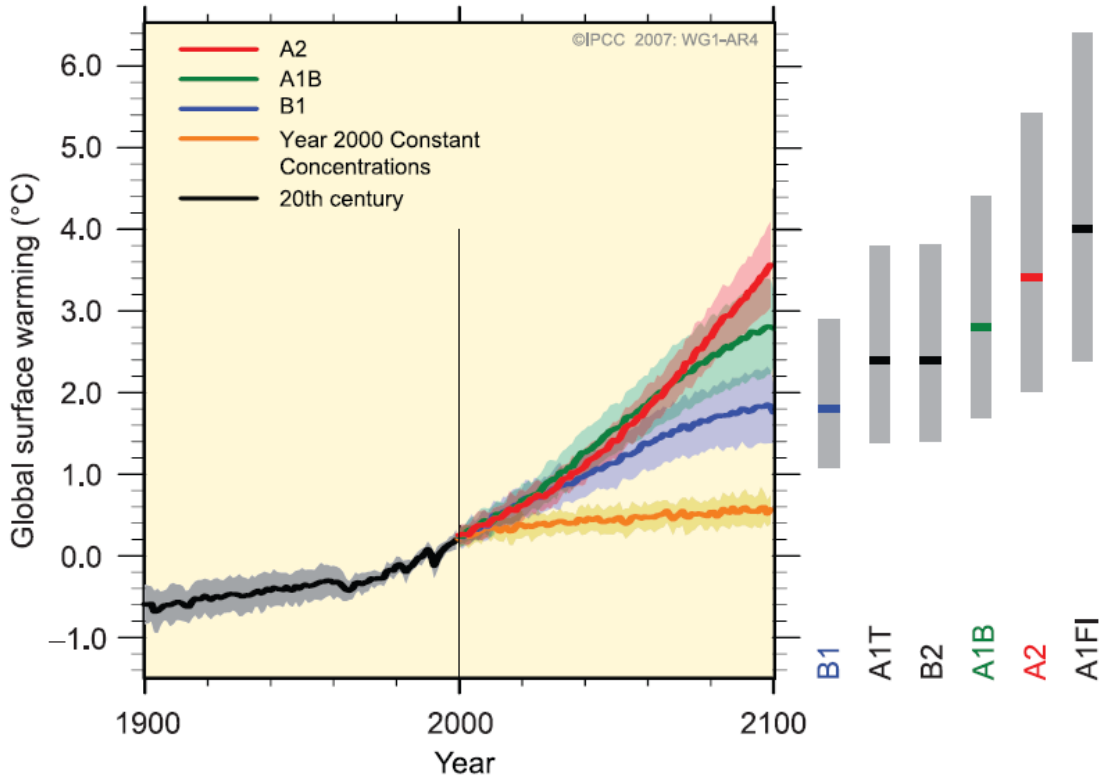


Table 3.1 Monthly temperature and precipitation predictions for three Atmospheric-Ocean General Circulation Models (AOGCMs) under emission scenario A1B (Nakicenovic et al. 2000) provided by NCAR. For each model, monthly changes in values of precipitation and temperature from a base-period (years 1980-1999) to 2030 (average change between 2020 and 2039), and from the base-period to 2080 (average change between 2070 and 2089) were provided by NCAR for an area approximately 5.6º in latitude and longitude in the Northern US Rocky Mountains.

	Wet		**Median**		**Dry**	
	cccma.t63		**PCM**		**gfd10**	
	Precipitation (%)	**Temperature (ºC)**	**Precipitation (%)**	**Temperature (ºC)**	**Precipitation (%)**	**Temperature (ºC)**
2030 (2020-2029)						
January	-15.99	1.21	-2.33	0.99	-6.51	0.32
February	23.16	1.93	4.43	0.77	-10.87	1.37
March	13.28	1.21	0.75	0.73	1.19	1.95
April	11.63	0.85	-0.12	0.47	11.8	1.03
May	21.03	1.44	7.41	0.79	1.62	0.21
June	18.01	0.61	7.99	0.83	-17.7	0.15
July	-2.92	0.88	-4.43	1.11	-32.36	3.17
August	15.95	0.44	3.92	0.9	-47.88	3.51
September	9.26	0.01	-17.01	1.28	0.38	1.68
October	17.15	1.1	13.87	0.8	-3.71	1.95
November	22.37	0.49	-3.92	0.55	0.81	1.51
December	22.83	1.71	-4.19	1.03	-1.82	1.2
2080 (2070-2089)						
January	4.52	3.38	6.95	3.84	-10.69	3.34
February	37.3	4.4	14.12	3.6	6.6	4.61
March	24.66	2.58	9.35	1.64	14.44	3.98
April	36	2.58	10.85	1.51	19.35	2.98
May	20.94	3.33	11	1.6	2.38	2.1
June	-6.83	2.85	11.79	2.5	-26.66	2.83
July	-9.16	3.08	-4.9	2.97	-50.35	7.5
August	-7.66	2.44	8.13	2.82	-47.16	8.52
September	16.7	2.5	-29.77	3.3	-40.71	5.48
October	13.25	3.04	12.96	2.26	-18.14	4.28
November	36.41	1.1	1.46	1.99	6.71	3.68
December	23.48	3.93	-3.9	2.72	31.55	3.25

The resulting monthly temperatures and precipitation predictions, from CGM3.1(T63), PCM, and GFDL-CM2.0under SRES scenario A1B (Table 3.1), were the basis for the three climate change scenarios under which I explored the effects of climate change on our forested sites. The climate change scenarios do not account for local differences, such

as the differences in climate change according to altitude or on the leeward and windward side of mountains. The selected AOGCMs differ in their precipitation and temperature projections only. In a general annual-based comparison to present-day climate, CGM3.1(T63) is the wettest model for both the 2030 and the 2080 change-periods, and is much wetter than present-day climate. GFDL-CM2.0 is the driest (much drier than present-day climate) in both the 2030 period and the 2080, and PCM is very similar to present-day total precipitation quantity in the 2030 period, although a little wetter, and mostly wetter than present day in the 2080 period. All three AOGCMs are warmer than present-day climate, with GFDL-CM2.0 being much hotter than present-day climate in the 2030 change period, and very hot in comparison to present-day climate in the 2080 change period. CGM3.1(T63) is warmer than present-day climate in both change periods, and PCM is a little warmer than the present-day climate in 2030 and warmer than the present-day climate in the 2080 change period. GFDL-CM2.0 distinguishes itself from the two other models, as it is much hotter and drier than our present climate. CGM3.1(T63), PCM, and GFDL-CM2.0 are referred to as wet, middle, and dry respectively in this text. Note that on a seasonal basis, there is much more variation between models than is described here.

Methods

Sites

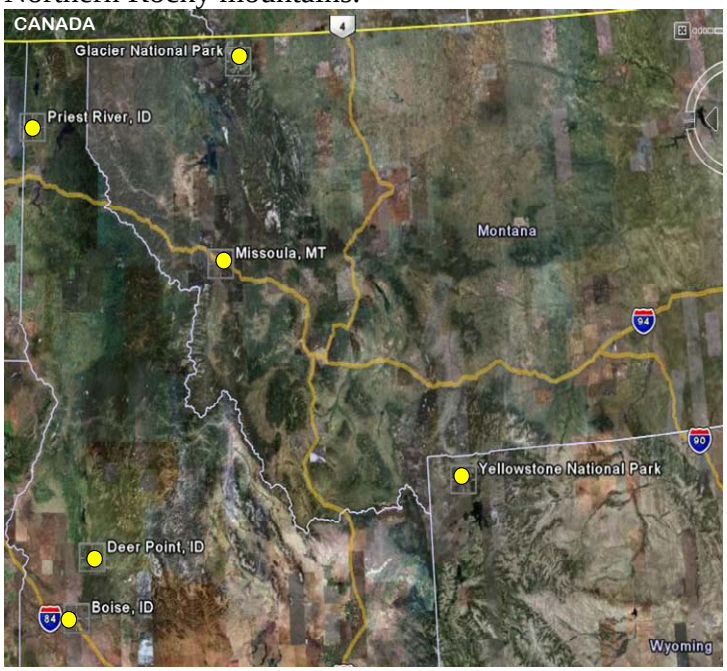
Six sites were strategically selected to represent climate niches across the wide range of elevation and historical precipitation in the US Northern Rockies region. Sites representing a range of elevation (a strong surrogate for temperature in mountainous terrain) and precipitation levels are listed in Table 3.2, along with their annual, winter, and summer average temperatures. Annual precipitation levels

Table 3.2 Elevation, annual, winter and summer average temperatures (1950-2005) for sites selected as representative of climate niches in the forests of the US Northern Rockies.

	Elev.	Precip.	Temperature (ºC)		
Sites	**(m)**	**(cm)**	**yearly**	**winter**	**summer**
Boise	857	30	14	2	26
Missoula	1042	44	10	-1	22
Yellowstone	1909	46	6	-6	18
Deer Point	2147	49	9	-2	21
Priest River	725	81	10	-1	21
Glacier	1600	107	5	-5	16

among the sites ranged from 30 cm/year to 192 cm/year between 1950 and 2005. Selected sites were: the city of Boise, ID, at 857m elevation, representing a grassland-forest ecotone; Deer Point weather station, located in the mountains northeast of the city of Boise at 2147m (high-elevation dry site); Priest River, ID, at 725m (low-elevation wet site); the Summit NCDC weather station in Glacier National Park, MT, at 1600m (high-elevation wet site); a station in Missoula, MT, at 1042m (low-elevation dry site); and the Tower Falls weather station in Yellowstone National Park, WY, at 1909m (high-elevation dry site) (Figure 3.5). Each site corresponds to National Climatic Data Center (NCDC) weather stations.

Figure 3.5 Six climate-niche sites selected for analyzing the effects of climate change on forests of the US Northern Rocky mountains.



Biome-BGC Inputs

Biome-BGC requires meteorological data, site characteristics information, and ecophysiological data to simulate biomes through time.

For each site, complete daily climate records were constructed from 1950 to 2005 using NCDC data. Daily surface records from NCDC for any climate stations are rarely complete; hence, to construct complete daily records, I used a combination of adjacent climate station data modified to fit the target station characteristics using the single-point bioclimatology model, MT-CLIM (Mountain Climate Simulator), as well as DAYMET, a model that generates daily surfaces of temperature, precipitation, humidity, and radiation over large regions of complex terrain (http://www.daymet.org/).

Using the provided monthly values of each AOGCM for each of the two time periods combined with actual climate data from 1950 to 2005, I constructed a time series of daily precipitation and temperature from 1950 to 2089. Conforming to AOGCM development, daily data from 1980 to 1999 for our six selected sites were used as a base period to which changes in precipitation and temperatures for 2030 (2020 to 2039) and 2080 (2070 to 2089) were applied. Linear interpolation of monthly precipitation and temperature values between 2005 and 2020, and between 2039 and 2070, were combined with daily to monthly variation from the last 15 and 30 years, respectively, of actual data (1992 to 2005 and 1976 to 2005) to complete the time series. Note that an application of time-series projection (e.g., Autoregressive integrated moving average - ARIMA) may have been a statistically more appropriate tool for such a projection, but in a trial, this approach did not produce significantly different results from the approach described here, and added seemingly unnecessary complexity to this preliminary step. Further, using a time-series projection would have veered away from the AOGCM development approach.

CO_2 levels, required as inputs to Biome-BGC, matched levels specified in the IPCC SRES A1B. Biome-BGC version 4.2 was used to project evergreen needle forests growing on our six sites, with adjustments to the ecophysiological parameters to suit each site, from 1950 to 2089 under each AOGCM, creating three projections of each of the six sites. Spin-up runs of Biome-BGC (i.e., model-runs over extended time periods) were used to provide the initial 1950 C and N state for each site. Soil inputs were generated using State Soil Geographic (STATSGO) data, which provides 8-km soil datasets, compiled by the Natural Resources Conservation Service (NRCS; http://www.ofps.ucar.edu/gcip/soils.html). Soil data were extracted based on the latitude and longitude for each site from STATSGO data. Industrial N deposition values were set at 0.0004 kgN m^2 $year^{-1}$.

Analyses

I completed the analyses by comparing carbon fluxes, such as Net Primary Production (NPP) and Net Ecosystem Production (NEP), actual carbon on site, and differences in

snow pack, growing season length, and number of water stress days between AOGCMs across sites and between sites.

NPP is a carbon flux defined as the photosynthesis of the system minus the respiration of primary producers (Chapin et al. 2006). It is but one part of the NEP, which takes into account heterotrophic respiration. NEP is the accumulation of carbon over a whole ecosystem and over a whole season or other time period (IPCC 2003), while NPP is the accumulation of carbon in the vegetation over a specified time period. NPP and NEP are useful measures of carbon at an ecosystem or forest stand level. Comparing the differences in these measures, along with total site carbon between sites and AOGCMs, permitted an analysis of the effects of the different climate scenarios on ecosystem-level carbon in the different forests of the US Northern Rockies.

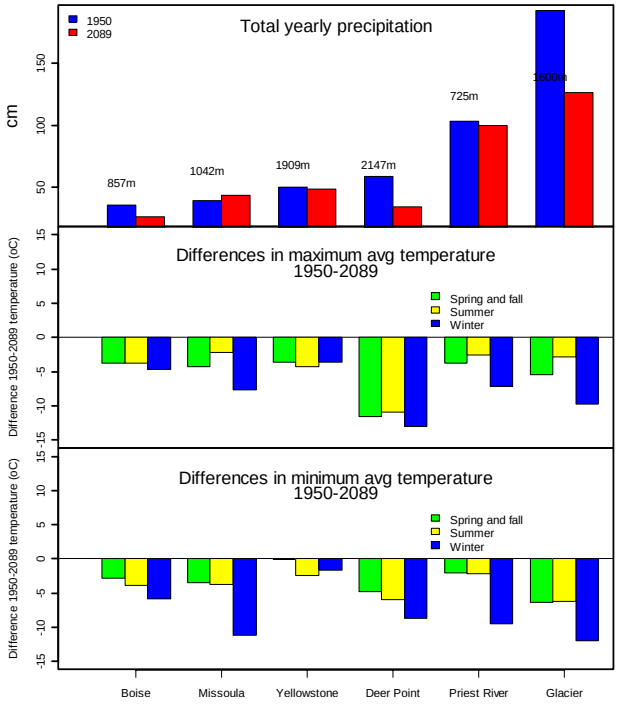
The water resources of the western US depend heavily on snow pack to store part of wintertime precipitation for use in the drier summer months (Knowles et al. 2005). Analyzing the trends and site differences in the number of water stress days, length of growing season, and the effect on snow pack of the different AOGCMs permitted a look at the water-carbon baseline under these scenarios. I defined a water stress day as a day on which water potential of soil and leaves reaches -1 MPa, a general stress level for conifers in the Northern Rockies. I looked at both the number of days with snow on the ground and the timing of the maximum amount of snow on the ground (peak snow) for each year, with a year defined as October 1st of the previous year to September 30th of the given year, with the exception of 1950, where the water-year is defined as January 1st, 1950, to September 30th, 1950, since 1949 data were not available. The concept of a growing season can be defined in many ways, all of which are arbitrary since a growing season is more of a continuum than a discrete event (Jolly et al. 2005), especially in conifers. For the purpose of this study, a constant definition was needed to provide a comparison point between the different time periods and different projections of climate. I defined the beginning of the growing season as the first period of more than seven days in a row with greater than 30% of the average maximum photosynthesis between 1950

and 2005, and the end as the first period of greater than seven days of photosynthesis below that threshold.

Results

Our constructed daily climate time-series (1950-2089), used as input to Biome-BGC, yielded annual average daily temperatures in Deer Point, ID, of 17ºC versus 8ºC in Glacier, MT, and average annual precipitation values from 111 cm in Glacier to 32 cm in Boise. The time series differentiated well between the sites, where drier sites such as Boise, Missoula, and Yellowstone were indeed drier and higher elevation sites (Deer Point, Glacier and Yellowstone) were colder. Figure 3.6 shows total annual precipitation and average maximum and minimum temperatures by season for 1950 and 2089.

Figure 3.6 Total yearly precipitation, average maximum, and average minimum temperatures by season for 1950 and predicted for 2089 for sites across the US Northern Rockies.



Results reveal that under all AOGCM projections and SRES A1B, between 2005 and 2089 across sites, growing season length (GS) increases, the number of days on which snow is present (SW) decreases, and the number of water stress days (WS) increases, all with significant linear trends (e.g., Figure 3.7). Average changes in growing season, snow water, and water stress per AOGCM across sites are shown in Table 3.3.

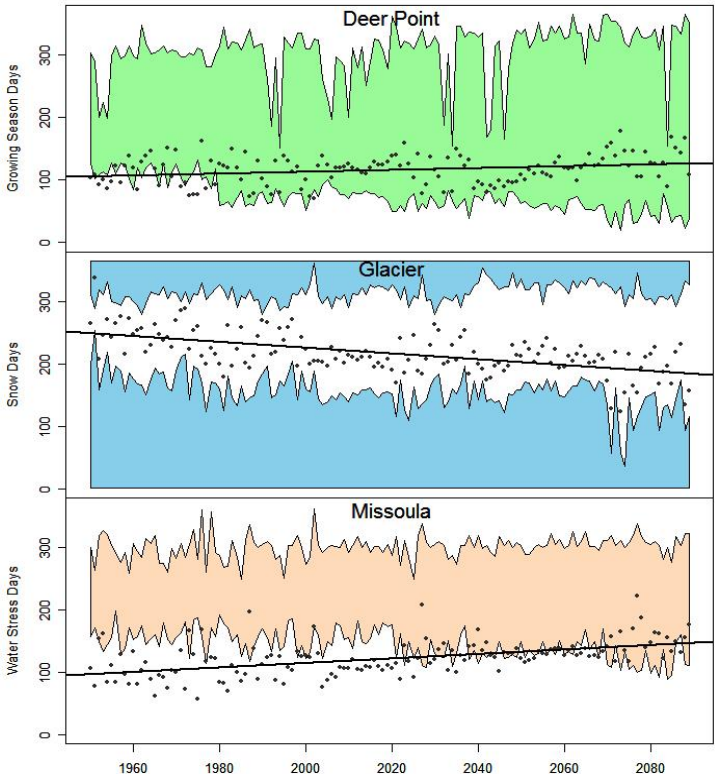
Table 3.3 Average number of days of increased growing season length , decreased number of days with snow water on the ground and water-stress days, by AOGCM model (Wet, Middle, Dry) across all sites.

AOGCM	Growing Season		Days with Snow		Water Stress	
	avg	sd	avg	sd	avg	sd
Wet	31	13	-50	52	56	17
Middle	22	10	-54	51	60	17
Dry	23	15	-67	47	67	16

The number of days where water potential of soil and

leaves surpassed -1Mpa (the definition of water stress for this study) did not show any linear trends between 1950 and 2005, and the number of days of water stress predicted by each AOGCMs between 2005-2089 differed very little between models. Hence, I compared the number of water-stress days above the 1950-2005 average number of water-stress days, across all AOGCMs, for the 1950-2005 time period and for the 2006-2089 time period. Figure 3.8 illustrates this comparison. Across all sites, the number of water-stress days increased by an average of 47 days. When I compared the number of water-stress days between 1950 and 2089, Deer Point increased the most, with 86 more days by 2089 of water stress under the wet AOGCM projections and 91 more days under the dry AOGCM projections and Priest River increased the least, with 37 and 48 more days of water stress by 2089 as compared to 1950, under the wet and dry projections

Figure 3.7 Projected growing season increase at Deer Point, ID, site, snow pack decline at Glacier, MT, and projected increase in water stress at the Missoula, MT, site under three AOGCM climate projections. The shaded areas show the timing of the growing season (green), the presence of snow (blue) and water stress (pink); the dots are the total number of days of growing season, snow presence, and water stress respectively, with a fitted linear model (line).



respectively.

For five out of six sites, peak snow (maximum amount of snow on the ground in a given snow year) occurs earlier by the end of the projection (2089) than it did at the beginning (1950). According to a linear model across the time series (1950-2089) and across all AOGCMs, peak snow occurred 29 days earlier on average for five of the sites, with peak snow occurring 54 days earlier at the Deer Point site, seven days earlier at Boise, 41 days earlier at Glacier, 10 days earlier at Missoula and 31 days earlier at Priest River by the end of the projection versus the beginning. Yellowstone showed no significant difference between the beginning and the end of the projections. Figure 3.9 shows the average timing of peak snow according to a linear model of all the peak snow estimates from AOGCM projections for Glacier, MT, and Deer Point, ID. The peak snow in Deer Point goes from February 14th in 1950 to December 23rd in 2089, and from April 8th in 1950 to February 25th in 2089 for Glacier.

Figure 3.8 Number of years where water stress (water potential of soil and leaves less then -1MPa) is above the yearly average number of water-stress days between 1950 and 2005 calculated as a proportion, for the 1950 and 2005 time period and for the 2006 to 2089 time period. Water potential of soil and leaves were modelled using Biome-BGC while climate projections followed three AOGCMs under emission scenario A1B used in the IPCC AR4.

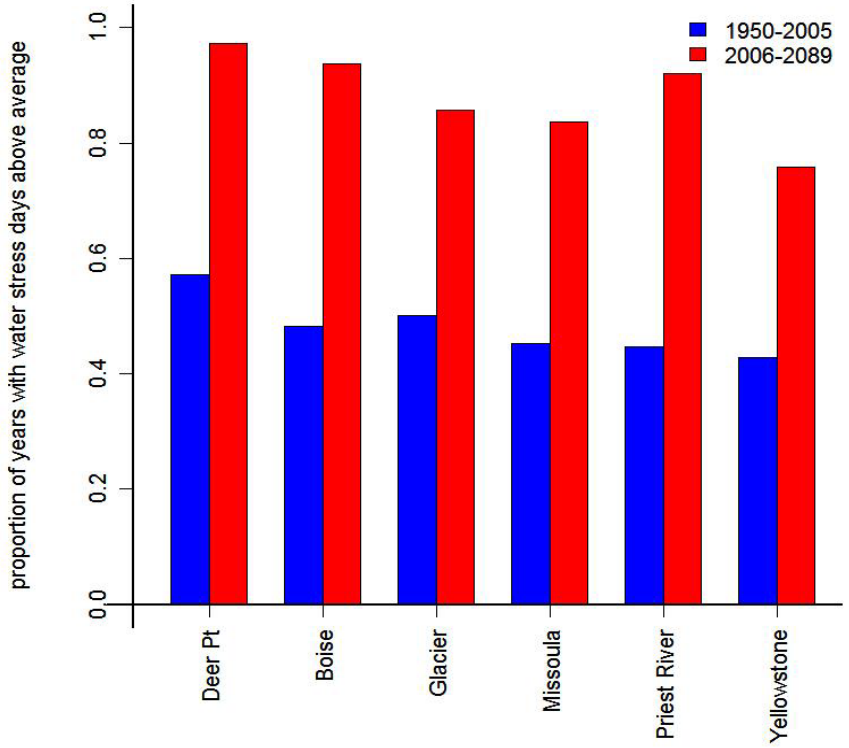
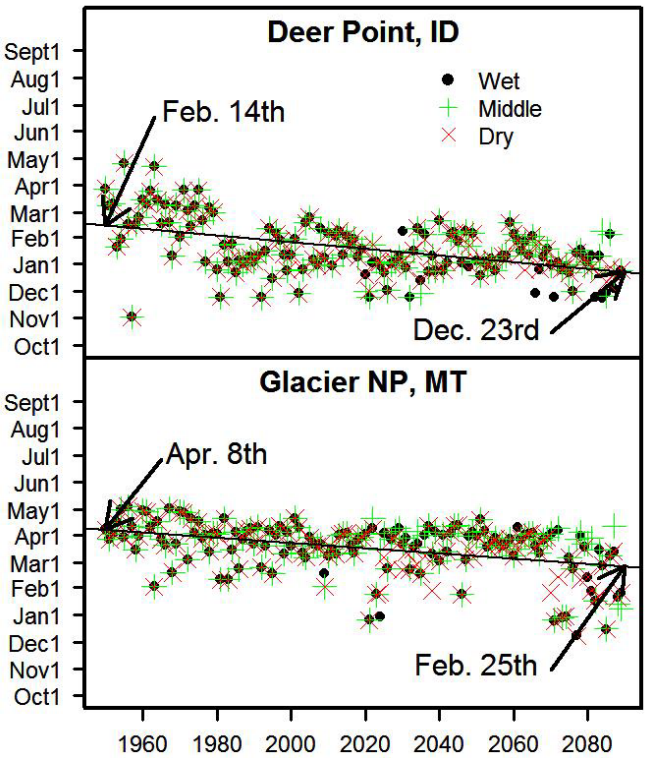


Figure 3.9 Timing of maximum amount of snow on the ground based on meteorological data (1950-2005) and AOGCM projections (2006-2089) for Glacier NP, MT, and Deer Point, ID.



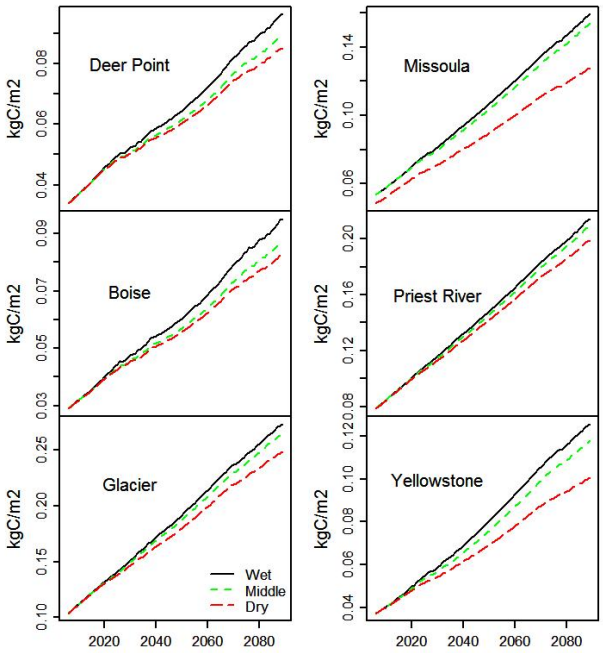
Based on the linear model of the total number of growing season days across the time series (1950-2089), I calculated the difference between the predicted length of the growing season in 1950 and that predicted in 2089. Table 3.4 lists those differences per site by AOGCM. The total growing season length showed a significant increasing linear trend for all sites and all models, except for Yellowstone under the dry climate projections, where the growing season length showed no trend. Under all three projections, the growing season length in Boise changed the most, with increases of 50, 35, and 43 days in the wet, middle and dry projections respectively, and Glacier showed the least change, with 19, 15, and 17 more days of growing season under the wet, middle, and dry projections respectively.

Table 3.4 Difference between the 1950 and the 2089 average growing season length (from a linear model) by AOGCM (Wet, Middle, Dry) for six sites across the US Northern Rockies.

	AOGCM		
Sites	**Wet**	**Middle**	**Dry**
Deer Point	33	20	30
Boise	50	35	43
Glacier	19	15	17
Missoula	41	34	27
Priest River	21	15	22
Yellowstone	20	14	NS

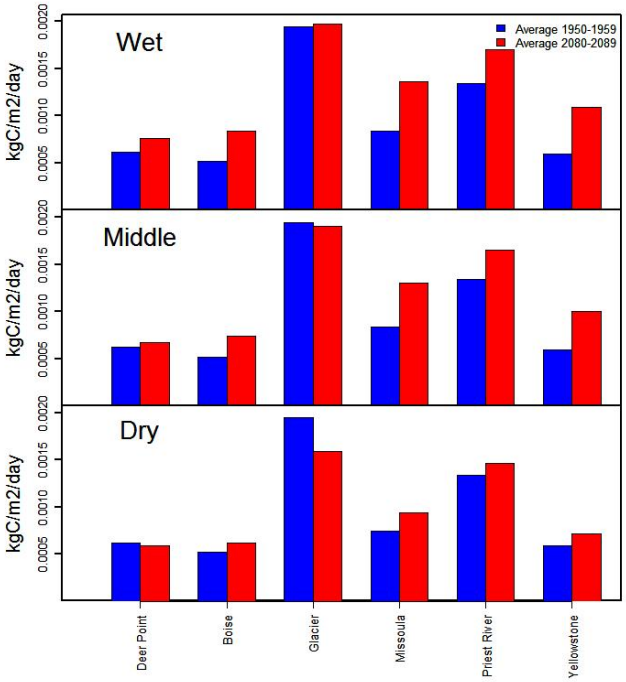
Carbon accumulation and carbon fluxes also responded to the climate

Figure 3.10 Cumulative NPP values for each of the six US Northern Rockies sites for three AOGCMs climate projections from 2006-2089.



projections, but unlike growing season, snow pack, and water stress, responses were more pronounced between AOGCMs. Figure 3.10 shows site specific differences in AOGCM projections for cumulative Net Primary Production (NPP). NPP for Missoula, Priest River, and Yellowstone increased under all scenarios, but much more under wet and middle projections than under the dry projections (Figure 3.11). Glacier NPP did not change much with wet and middle projections, but declined under the dry projections. Boise and Deer Point NPP increased slightly with CGM3.1(T63) and PCM, but there was no change in NPP under the dry projections (Figure 3.11). NPP had a significant negative correlation with water-stress days, while respiration had a significant positive correlation with water stress days across all sites for all AOGCMs (Table 3.5). Across all sites, at a site level, total site carbon under the dry projections lags behind the wet and middle projections (Figure 3.12).

Figure 3.11 Average NPP predicted by Biome-BGC for the 1st 10 years (1950-1959) and the last 10 years (2080-2089) of simulations for six US Northern Rockies sites under three AOGCM climate projections.



Net Ecosystem Productivity (NEP) values for the two projected time periods that matched the AOGCM projections (2020-2039 and 2070-2089) were used to calculate whether sites were carbon sources (NEP<0) or carbon sinks (NEP>0) during those time periods. As illustrated in Figure 3.13, from 2020 to 2039, 3/6 sites are carbon sources with dry-AOGCM climate projections, one with middle-AOGMC, and none with wet-AOGMC, while from 2070 to 2089, 5/6 sites are carbon sources with dry-AOGCM climate projections versus 1/6 with the other AOGCMs.

Table 3.5 Correlations between NPP and water-stress days and respiration and water-stress days for six sites across the US Northern Rockies under three AOGCM projections.

		AOGCM		
Sites	**Variable**	**Wet**	**Middle**	**Dry**
Deer Point	**NPP**	-0.45	-0.54	-0.62
Boise		-0.42	-0.44	-0.53
Glacier		-0.43	-0.48	-0.58
Missoula		-0.26	-0.28	-0.50
Priest River		-0.18	-0.21	-0.39
Yellowstone		-0.19	-0.18	-0.34
Deer Point	**Respiration**	0.37	0.27	0.27
Boise		0.38	0.39	0.36
Glacier		0.58	0.55	0.49
Missoula		0.44	0.44	0.40
Priest River		0.55	0.56	0.56
Yellowstone		0.40	0.46	0.50

Figure 3.12 Total site carbon based on Biome-BGC projections under three climate change scenarios for six sites across the US Northern Rocky Mountains from 2006-2089.

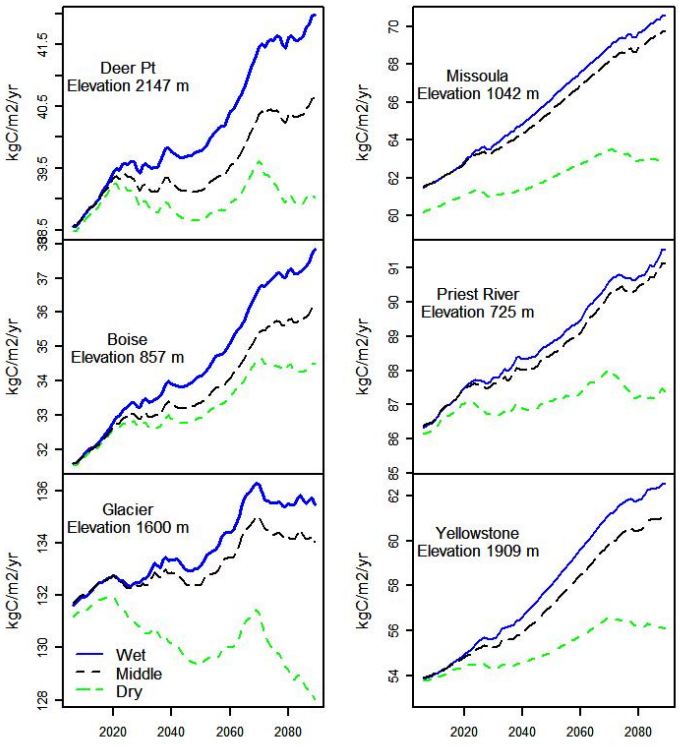
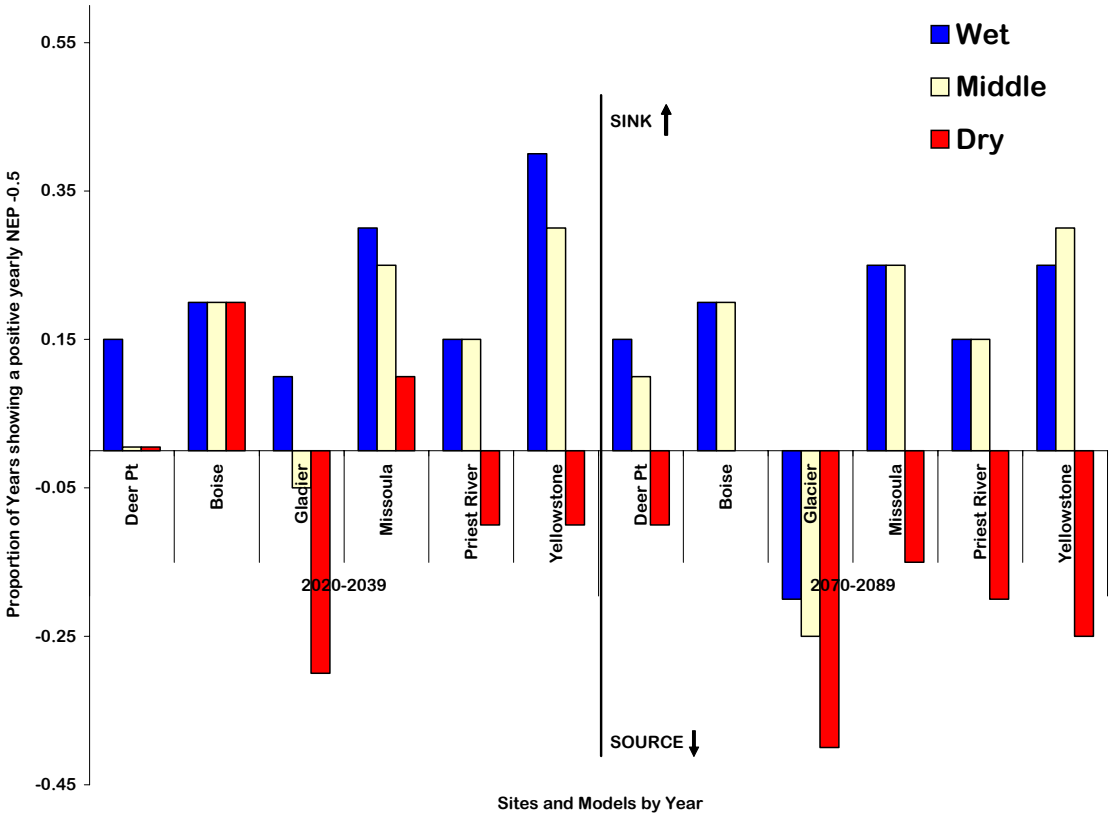


Figure 3.13 Proportion of years during which Biome-BGC projections of six US Northern Rockies sites, under three AOGCM climate scenarios, showed a positive NEP, minus 0.5, during the 2020 to 2039 and the 2070 to 2089 times periods. Sites above 0 mark a carbon sink, while sites below 0 mark carbon sources.

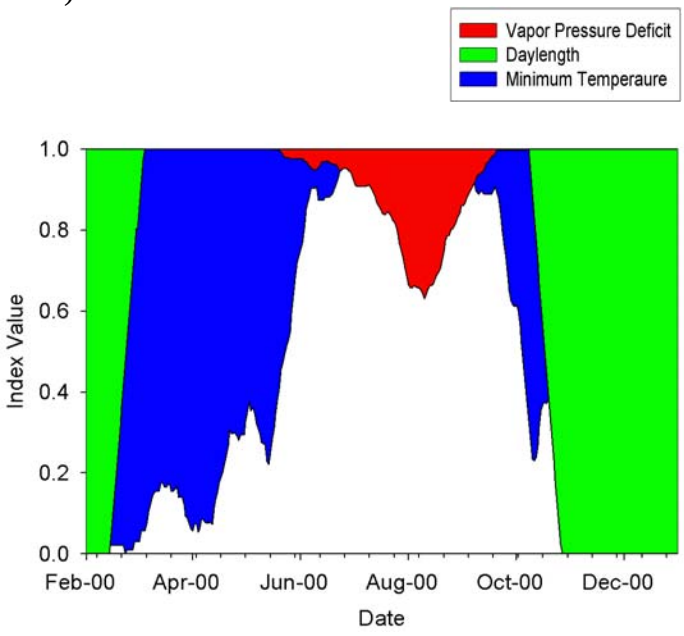


Discussion

Biome-BGC emulates the effects of the main drivers of and constraints on ecosystem productivity: light, water, and temperature. Like many regions of the world, the Northern Rocky Mountain region of the US is subject to each constraint in turn, at different times of the year. As an example, Figure 3.14 visually displays the most prominent constraints throughout the year 2000 for Missoula, MT. From Figure 3.14, we can see that in Missoula, day length is the primary constraint from November to February, low temperatures constrain productivity in late winter, spring, and fall, and water stress limits productivity in the warm months of summer. During the bulk of the growing season, when light and low temperatures are not limiting, water drives the system. In this respect, many sites across this portion of the Rocky Mountains behave like Missoula; overall

productivity depends on moisture conditions during the main part of the growing season. Spring, summer, and autumn temperatures, summer precipitation levels, and the previous winter's snow pack determine summer moisture conditions.

Figure 3.14 Seasonal productivity constraints for Missoula, MT throughout the year 2000 (Jolly et al. 2005).



Net Primary Production (NPP) has been shown to correlate positively with precipitation levels (Knapp and Smith 2001, Kang et al. 2006). Soil moisture is the link between precipitation and forest ecosystems (Weltzin et al. 2003). Generally, in the temperature ranges of the US Rocky Mountains during summer months, as long as soil water is available during the growing season, stomata stay open and photosynthesis occurs. Stomata close under limited water conditions, halting the photosynthesis process. When water is not limiting, annual photosynthesis in these conifer forests is controlled by atmospheric conditions via their influence on absorbed photosynthetically active radiation (PAR) and the effects of available light and temperatures on stomatal conductance (Waring and Running 1998). Water stress suppresses photosynthesis, by reducing light-use efficiency, and respiration, by limiting growth and/or suppressing microbial respiration (Barr et al. 2007). Increases in growing season length due to increases in temperatures (as our results show and as is already reported elsewhere (Menzel et al. 2006)) may result in increases in productivity, specially in high latitudes, where temperatures constrain productivity in certain parts of the year. A small part of this productivity increase may be caused by temperature increases alone (Bergh et al. 2003); phenotypic plasticity may buffer the effects of changes in soil moisture regimes on productivity and thereby increase the resilience of ecosystems to reduced precipitation, but the potential for this buffering effect is not known (Weltzin et

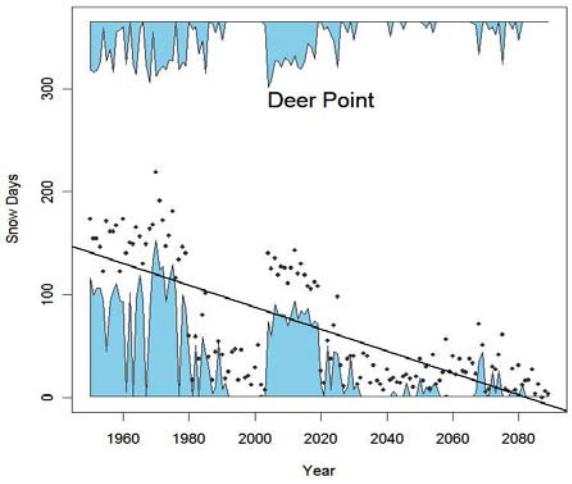
al. 2003). Dang et al. (2007), Min and Guang-Sheng (2006), and White et al. (2006) all identified temperature as a driver of productivity in their studies.

This lengthening of the growing season, however, may exacerbate the summer drought episodes illustrated in Figure 3.14. In general, warmer springtime temperatures result in increased net CO_2 uptake only if adequate moisture is available; when warmer springtime conditions lead to mid-summer drought, the annual net uptake declines (Sacks et al. 2007, Bergh et al. 2003). Not high temperatures, but the accompanying drought stress, caused the decline in productivity that followed the 2003 European summer drought (Reichstein et al. 2007). Droughts can even influence continental-scale carbon gain (Ciais et al. 2005).

The differences in carbon fluxes and total carbon in my results can be explained by changes in growing season length, snow water, and water stress alone, without accounting for CO_2 increases or other changes. Their individual effects, however, cannot be disentangled in our projections, as they are interdependent. Results showed limited productivity increases under the three selected climate-change scenarios despite increases in growing season length, suggesting that in our systems, water drives productivity. Simulation results showed a one- to three- month increase in water-stress days across all sites. NPP was negatively correlated with the number of water stress days but generally increased with wet- and mid-AOGCM climate projections, although much less under the dry climate projections, where NPP even decreased in Glacier (Figure 3.11). This decrease in productivity in Glacier, the highest-productivity site of the six, suggests that under the dry climate-change projections, sites like Glacier (high-elevation wet sites) will decrease in productivity under the dry climate projection. This decrease may not only be due to the water-related reduction illustrated in Figure 3.14 for Missoula, but may also result from an increase in respiration in sites like Glacier that carry high quantities of biomass and winter snow. The summer drought period seems to have intensified, limiting the potential positive effects of a longer growing season across our sites.

The importance of snow pack water storage in the mountainous West is well known (Sheffield et al. 2004). With up to 75% of all stream water being made up of snowmelt, the role that cold-season processes play in the development of summer drought and fire risk cannot be underestimated (Service 2004). A well-documented shift towards earlier runoff in recent decades has been attributed to more precipitation falling as rain instead of snow, and earlier snowmelt (Knowles et al. 2005). Growing seasons at Niwot Ridge, a high-elevation site in the Colorado Rockies (Sacks et al. 2007), were correlated with less net CO_2 uptake, due to a decrease of available snow-melt water during the late springtime photosynthetic period. Simulation results showed a continuation of these trends with, on average, one month earlier peak snow across all sites and significant negative linear trends in the number of days with snow on the ground per year (e.g., Figure 3.15). Less snow will likely increase the summer-drought period, further increasing the number of water-stress days, as results show. At those dry sites that presently depend on their snow pack to maintain a forest canopy during summer months (such as represented by Deer Point and Missoula), simulations indicate that by 2089, under all three GCM projections, there would be very little to no snow pack left on these sites. Boise, a site representing the ecotone between forests and grasslands, has already recorded only 16 days with snow on the ground in 2005, with an average of 27 days, ranging from 84 to 4 between 1950-2005.

Figure 3.15 Projected snow pack decline at Deer Point site. The shaded areas show days with snow in a calendar year, the points are the total number of days with snow on a given year, and the line is a fitted linear model through the total number of days with snow per year.



Under dry-AOGCM climate projections, total carbon on site is reduced for all sites: a water/temperature-driven tipping point, past which system carbon drastically declined, seems to exist. This tipping point is visible in Figure 3.12 for all sites in the difference between dry projections (green) and the wet and middle climate projections. As described in the background section, all AOGCM projections are warmer than present-day

climate, but the dry AOGCM projection is also much warmer than present-day climate. This temperature and precipitation scenario showed a stabilization or slight decline in total site carbon at our Boise, Missoula, Priest River, and Yellowstone sites while it showed a decline at our Glacier and Deer Point sites (Figure 3.12). The other two scenarios show increasing total carbon for all sites. At the driest sites (Boise and Deer Point), projections are equidistant in carbon accumulation, signaling a higher sensitivity to combinations of precipitation and temperature in each of the models. Projections from the wet and middle AOGCM are much more similar for the other sites, suggesting that the difference in temperature and precipitation between the wet and middle AOGCMs does not affect these sites as drastically. The most productive site, the high-elevation wet forests represented by Glacier, shows the most drastic decline in total carbon accumulation, and both Glacier and Deer Point (representing the high-elevation dry forests of the US Northern Rockies) show the most pronounced decline in carbon accumulation. According to these projections, if the future precipitation and temperature scenario is similar to or drier than the dry scenario depicted here, forests at both ends of the spectrum of productivity may reduce their carbon accumulation. Forests even become carbon sources near the end of the time series under the hot/dry conditions projected by the dry-AOGCM (Figure 3.13), similarly to what the projections of Morales et al. (Morales et al. 2007) predicted for European ecosystems by 2100.

It is important to note that year-round NEP values were the basis for Figure 3.13, where sites are depicted as sources or sinks in two time periods. These values were not constrained by our initial definition of growing season. They include year-round simulation of NEP, and there can be substantial respiration under snowpacks in winter (Bergeron et al. 2007), which may explain Glacier, a present-day high-productivity site, becoming a carbon source sooner then the other sites. Again, the balance between winter temperatures and snow pack may play an important role in determining if a site is a carbon source or sink over winter. Anthoni et al. (1999) showed a 40% gain of annual carbon in a ponderosa pine forest occurring outside the traditional growing season, a time with temperatures below freezing and high snow accumulation. In contrast, Sacks et al. (2007) found high-elevation forests to have down regulated, becoming a carbon source

under cold (although colder than Anthoni et al.) and snowy conditions. It seems that not only can earlier snow melt lower annual carbon gain due to summer soil moisture limitation, but winter snow pack and temperature may also play into site carbon accumulation.

Changes in growing season, water stress, and snow water, driven by the combined temperature and precipitation changes, intermix with the effects of increased CO_2 in our simulations. There is published evidence of a CO_2 fertilization effect on forests (Moore et al. 2006). In a simulation exercise, Mu et al. (submitted) found that climate change alone reduces carbon storage in China's ecosystems, but increasing CO_2 levels compensate for the adverse effects of climate change. The CO_2 fertilization effect, however, is increasingly qualified; Bergh et al. (2003) identified CO_2 effects as species specific; Yude et al. (1998) identified many factors influencing response to elevated CO_2, such as VDP levels, N deposition, cloud cover, etc.; and Bytnerowicz et al. (2006) assert that combined effects of pollution and climate change can change responses.

Results from Free Air CO_2 Enrichment (FACE) sites around the world, a method and infrastructure used to experimentally enrich the atmosphere enveloping portions of a terrestrial ecosystem with controlled amounts of carbon dioxide, present varied responses to CO_2 increases. A FACE site in Wisconsin, US, found CO_2 to increase but O_3 to decrease aboveground NPP, hence, investigators could report no detectible response to CO_2 and O_3 in the high-NPP response to interannual climate variability (Kubiske et al. 2006). Ozone effects are not incorporated in Biome-BGC simulations, but high O_3 levels damage the photosynthesis apparatus and have been reported to reduce productivity (Ashmore 2005, Cojocariu et al. 2005, Oksanen et al. 2005, Sitch et al. 2007), although high O_3 levels have not been an issue in the US Northern Rockies as defined here. A FACE site in Basel, Switzerland, reported that stem growth after 4 years of exposure does not support the notion that mature forest trees will accrete wood biomass at faster rates in a future CO_2 enriched atmosphere (Asshoff et al. 2006), while (DeLucia et al. 2005) reported an increase in productivity under CO_2-enrichment at a FACE site in North Carolina, US. These contrasting responses to elevated CO_2 may correspond to the

different development stages of these respective sites, as disturbance history and stand age also play into the response to elevated CO_2 (Ollinger et al. 2002, McIntire et al. 2005, Albani et al. 2006). Thornton et al. (2002) even reports Net Ecosystem Exchange to be largely a function of disturbance history, with important secondary effects from site climate, vegetation ecophysiology, and changing atmospheric CO_2 and N deposition. These findings illustrate the complex response of forests to elevated CO_2. This complex response has not yet been defined, and clearly multiple factors interact.

One factor is N deposition. Nanus et al. (2003) mapped N deposition levels across the Rocky Mountains. In the simulation used in this study, wet and dry natural N depositions were set at 0.004 kgN/m^2/year, with industrial deposition set at 0.0004 kgN/m^2/year, across all sites. Although these settings are within historical ranges, they do not match those specified by Nanus et al. (2003). The generalized nature of this study, with broad climate projections and no species or age specification, did not seem to warrant the use of precise N deposition rates, which vary by elevation, slope, aspect, and precipitation amount and by regional and local sources of air pollution. Maps indicate an increasing spatial trend in concentration and deposition of the modeled constituents, particularly nitrate and sulfate, from north to south throughout the Rocky Mountains, trends not accounted for in my projections. Both this omission and our limited understanding of the physiological response of forests to elevated CO_2 and N deposition contribute bias to the projections presented here.

The intention of this exercise was to provide a baseline of the possible effects of climate projections with varying precipitation levels on forests in the US Northern Rockies. The logic incorporated in Biome-BGC (green-sponge, ageless systems, with no species specification), which permitted the tracking of changing climate effects for general forest types (like evergreen needle forests), was driven by uniform monthly projections of temperature and precipitation changes over a large geographical area. The scale of these projections does not reflect reality. Model predictions cover an area ~ 480 km (~300 miles) across. Forest ecosystem modelers must choose how to simplify and internally represent the real-world system under study, and their choices constrain subsequent

model use (Jackson et al. 2000). Hence, until reliable higher-resolution climate predictions are available, using Biome-BGC (a model designed to simulate biome responses to environmental changes on a regional scale) to model representative sites should provide an acceptable baseline of the effects of climate change on forests in this region.

The consequences of the amount of water on sites reach beyond productivity levels. In years where water is scarce, not only do forests become less productive and slow their nutrient cycling processes, but they are also under stress, which increases the likelihood of a suite of possible disturbances such as pest epidemics, wildfire, and general forest mortality. The baseline presented here does not incorporate any of these effects. Water stress levels and snow pack levels, the two main predictors of wildfire vulnerability, have also been related to insect outbreaks (Richard et al. 2002) (Collins et al. 2006). Historical fire activity generally resulted in reductions of both NPP and NEP (Kang et al. 2006). Large wildfire activity increased suddenly and dramatically in the mid-1980s in the Northern Rockies forests (Westerling et al. 2006). Reduced winter precipitation and an early spring snowmelt, as depicted in our simulations, played a role in this shift. The vulnerability of western U.S. forests to more frequent wildfires due to warmer temperatures is a function of the spatial distribution of forest area and the sensitivity of the local water balance to changes in the timing of spring (Westerling et al. 2006), and according to our results, US Northern Rockies forests are very sensitive to change in the water balance. Schumacher and Bugmann (2006) predict that fire is likely to become almost as important for shaping the landscape as the direct effects of climate change, even in areas where major wildfires do not occur under current climatic conditions.

Changes in species composition or even change in biomes may result from climate and disturbance regime changes. Other published studies have already predicted (Hamann and Wang 2006, White et al. 1998, Sefcik et al. 2007) or detected changes in composition (Jump et al. 2006) due to climate change. Changes in stochastic patterns of a variable environmental factor, such as precipitation, may have potentially stronger effects on ecological systems than do changes in average conditions or changes in other factors that

are relatively stable over time and space (Weltzin et al. 2003). Increases in drought-induced mortality (Gitlin et al. 2006) and wildfires (Westerling et al. 2006) would contribute to more rapid onset of this change. Sites similar to Boise, on the edge of the grassland forests ecotone, are already hovering close to non-forested precipitation levels (average between 2006 and 2089 of 30 cm/yr).

Although Chen et al. (2003) found overall positive effects of non-disturbance factors (climate, CO_2, and nitrogen) outweighed the effects of increased disturbances in the last two decades, making Canada's forests a carbon sink in the 1980s and 1990s, accounting for disturbances could drastically change the baseline findings presented here. Time since disturbance also influences carbon exchanges on sites (Law et al. 2001, Magnani et al. 2007), as do management regimes (Briceno-Elizondo et al. 2006) (De Vries et al. 2006) and stand age (Yarie and Parton 2005, Chen et al. 2002), none of which is incorporated in the baseline projections presented here.

The differences between the climate models used in our projections represents the minimum of uncertainty about regional climate change.

Conclusion

Projections of three AOGCMs with varying precipitation levels demonstrated the forests of the Northern US Rockies to be highly sensitive to the amount of water on site. Under all three climate scenarios, growing season lengthened, the number of days with snow on the ground decreased, snow peak occurred earlier, and water stress increased as compared to 1950 to 2005 for all sites. The drier climate projection revealed a water-temperature tipping point where total site carbon ceased to accumulate, and this scenario was more pronounced for sites at both ends of the productivity spectrum, the low-elevation dry and the high-elevation wet forests. Under the drier climate projections, most forests became carbon sources by the end of the projection.

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Chapter 2

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